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TOP-WORKING IN CUSTARD APPLES (*ANNONA SQUAMOSA* L.)

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CUSTARD apple (*Annona squamosa* L.) grows wild in a state of naturalization in the Telangana region of the Deccan Plateau in India. It is a drought-resistant tree, flourishing in gravelly soils in warm dry regions on slopes of hillocks and on waste lands. Tropical America is considered to be the home of Annonaceous fruits ; a few species are also found in Africa and some have been introduced into Southern California and Florida. They are also grown to a limited extent in Egypt, Ceylon and Java. In India, Annonaceous species occur commonly in the Deccan Plateau and in some parts of Central India. They prefer a dry climate and do not withstand severe low temperature.

Seedling material of custard apple is highly variable so that, though the trees grow readily even in the poorest soil, fruitgrowers have not yet recognized this crop as one deserving inclusion in their orchards. Most of the existing seedling trees are unproductive and bear inferior types of fruits. Among 132 trees at the Fruit Research Station, Sangareddy, only 15 were found to be inherently high-yielding. The vast plantations found in forests are mostly low-yielding. Trials on top-working such unprofitable seedlings to superior strains were initiated in 1954.

Popenoe (1934) suggested top-working as a means of overcoming unproductiveness in cherimoyer (*A. cherimola*) plants. It has been recorded that cherimoyer can be top-worked by means of cleft-grafting on Bullock's Heart rootstock (*A. reticulata*) and cherimoyer.

Materials and methods.

A seedling plantation of custard apple planted in 1943 at the Fruit Research Station, Sangareddy, was used in these studies. These unproductive custard apple trees were top-worked with Atemoya, a hybrid between *A. cherimola* and *A. squamosa*. Atemoya seedlings on custard apple rootstocks were also reciprocally top-worked with buds from high-yielding strains of the custard apple clone Washington 98797. Shield buds without wood were inserted. The buds were kept covered with thin strips of banana fibre for about a fortnight and later the eye of the bud was exposed by untying the banana fibre bandage.

After pruning, the trees were whitewashed to protect them from the summer sun. The cut ends were painted with paraffin wax coating after applying Bordeaux paste.

A preliminary trial indicated that trees cut back at six feet from the ground produced long shoots, most of which were subsequently broken by wind. Other trees cut low down to about six inches from ground level did not survive. Trees cut back to about three feet gave the best results and this height was therefore adopted for the main experiment (Figs. 1 and 2).

Large-scale trials of top-working were conducted on 65 custard apple trees. The trees were cut back on 24th February 1955 to 2½-3 feet from ground level, leaving four to six scaffold branches. The sprouted shoots were shield-budded in October 1955 when they had attained about one centimetre thickness. The buds started growth in January 1956. In that month unsuccessful branches were rebudded (Fig. 3).

RESULTS.

The number of trees top-worked and the proportion of successful buddings are shown in Table I.

TABLE I.

Percentage success of budding with Atemoya.

Month of budding	No. of trees budded	No. of buds inserted	No. of buds sprouted	Percentage success
October 1955	65	609	400	65·7
January 1956	58	232	173	74·6

The shoots started flowering sparsely in March 1956, but no fruit developed in the first year. Growth measurements were made in April 1956.

In the large-scale trial, 25 three-month-old shoots were measured for length and girth at the base. The average length was 62·2 cm. and girth 3·67 cm.

Similar trials of top-working Atemoya with buds from a high-yielding tree of Washington 98797 custard apple were initiated. Five trees were cut back in March 1955 and the sprouts budded in the following October. The unsuccessful ones were again budded in February 1956. The observations regarding the bud-take are detailed in Table II.

TABLE II.

Percentage success of budding Atemoya with Washington 98797.

Month of budding	No. of buds inserted	No. of buds sprouted	Percentage success
October 1955 ..	52	7	13·46
February 1956 ..	158	130	82·32

The measurements were made in December 1956. All the trees developed many lateral shoots and profuse blossoms which yielded some crop. Table III shows the average yields of top-worked trees.

The custard apple (Washington 98797) current year shoots had produced a well-shaped top in the first year with a fair crop of fruits. The leaves were dark green, stiff and the top was bushy. The size of the fruits varied from 5 to 14 oz. and the maximum yield recorded in the first year by one tree was 10 fruits totalling 4 lb. 11 oz.

TABLE III.

Average yields of top-worked trees.

Particulars of trees	Average length (cm.)	Average diameter (cm.)	No. of lateral shoots	November-December 1956		Off-season crop August 1957		November-December 1957	
				No. of fruits	Weight (lb.)	No. of fruits	Weight (lb.)	No. of fruits	Weight (lb.)
1. Atemoya on custard apple cut back 6 feet above ground level in 1954	208	5·9	20	3	2·1	0	—	10	6·1
2. Atemoya on custard apple 3 feet above ground level in 1954	244	4·4	16	5	3·4	0	—	6	3·7
3. Atemoya on custard apple (Washington 98797) in 1955 and 1956	116	2·5	5	0	—	0	—	1·7	1·0
4. Custard apple (Washington 98797) on Atemoya in 1955 and 1956	113	2·8	13	7·8	3·9	14·6	5·2	28	11·0

The fruits were a deeper ashy green than the original Washington fruits and possessed bigger areoles. They were also distinctly more juicy and less seeded. It thus appears that Atemoya as a rootstock imparts extra vigour and productivity to the custard apple scion.

An off-season crop was also obtained in August 1957, one tree giving a record yield of 51 fruits weighing 18 lb. 14 oz. Besides this a normal crop was obtained in October 1957. The maximum yield recorded by one tree was 60 fruits weighing 23 lb. 10 oz. The fruits had more flavour and juice and were bigger than normal custard apple fruits.

Atemoya scions top-worked on custard apple rootstocks started bearing in the second year of top-working. The fruits did not show any appreciable changes except for the disposition of areoles which were more squamose, as in custard apple. The furrows in between areoles were also more pronounced, resembling the custard apple.

DISCUSSION.

Top-working has often been used in perennial fruits to convert inferior and unproductive trees into superior ones. Such methods have been devised in mango, citrus, bet (*Zizyphus*) and deciduous fruits like apples, pears, etc., by several workers. Top-working in Annonas has been practised in the United States of America, mostly by cleft-grafting. In India, however, such studies had not been initiated.

The bud-take of custard apple trees worked at six feet was successful, but frequently the shoots had to be supported against high winds. Despite this many sprouted shoots broke away so that a strong framework could not easily be built up at such a height.

In the second method of top-working reported in this paper, the scaffold branches were cut back to three feet from ground level. These branches gave rise to vigorous shoots in six to eight weeks, which in turn were budded when they were half a centimetre thick. The bud-take was as good as when the trees were only cut to six feet, but there were no casualties due to winds, and a strong framework was secured. Atemoya shoots generally have a tendency to grow into long whips. In the first year these grew to 100-150 cm. in length. These were pruned to about 25 cm. from the tip to stimulate development of lateral branches. In the second year these shoots grew another 100 cm. producing lateral branches with a bushy top. The base of the shoots attained a girth of 3-6 cm., depending upon the position of the shoot on the tree.

Atemoya top-worked on custard apple came into bearing in the second year. The fruits were light green in colour and the areoles resembled those of custard apple and were of squamose type. In all the other fruit characters there was no appreciable change which could be attributed to the rootstock.

Atemoya as a rootstock seems to impart extraordinary vigour and precocity to custard apple scions. Topworked, the shoots developed strongly, producing both a sizeable main crop and an off-season crop in the first year. The fruits were of good size with a high pulp to seed ratio, 20:1 as against 12:1 in normal fruits. The areoles became wide and prominent and the fruits, as well as the foliage, deep green. In the second year a high yield was obtained in the regular season as well as in the off-season, a result which is uncommon in existing plantations.

PLATE I

Fig. 1.

Top-working Atemoya (*Annona cherimola* × *A. squamosa*) on custard apple seedings, in different stages.

Fig. 2.

A successfully top-worked *A. squamosa* with Atemoya scion.

Fig. 3.

A plantation of top-worked Atemoya in different stages of growth.

[*face page 4*

Pruning has been advocated just before the bud break, lest very early pruning should result in the death of the tree. In Guatemala, pruning is advocated just after the leaves begin to drop. At Sangareddy, Annonas are usually dormant from December to January. Therefore pruning was done during the last week of December and the new sprouts budded in April three months later. In a month's time the buds started sprouting and attained good growth during the subsequent growing season. In the budding trials at Sangareddy, the optimum periods for budding were February to June and again in September-October (Venkataratnam and Satyanarayanaswamy, 1956).

The buds inserted in October remained dormant and sprouted in January, whereas plants budded from January to June sprouted in a month's time. Therefore, pruning in April and May is found to be the best practice for top-worked trees. The bud-sprouts start flowering in the next season. In custard apple top-worked on Atemoya fruiting commenced in the first year, whereas Atemoya top-worked on custard apple rootstocks did not yield fruits until the second year.

SUMMARY.

(1) Top-working in Annonas with custard apple (*A. squamosa*) and Atemoya (*A. squamosa* × *A. cherimola*) was found feasible by using shield-buds without wood.

(2) Cutting the trees back to three feet from ground level was the optimum height for securing a strong framework with a well-shaped tree.

(3) Pruning in January and budding in April gave the best results on top-worked trees in the Deccan tract.

(4) Custard apple on a vigorous rootstock like Atemoya came into bearing in the following season, whereas Atemoya on custard apple rootstock only did so in the second year.

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SEED FERTILITY OF EDIBLE BANANAS

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CHEESMAN and Dodds (1942) recorded the results of pollinating eighteen triploid banana clones (3x = 33) with a number of diploid wild species of *Musa* (2x = 22). Only five were completely sterile : four members of the Cavendish group of somatic mutants (Cheesman *et al.*, 1933) and one other clone, Celat (Type 14). The others all yielded seeds, at least when crossed with *M. acuminata*. Few seeds were viable and the progenies were various mixtures of diploids, aneuploids, triploids, tetraploids and heptaploids, the last two classes evidently resulting from restitution nuclei in the megaspore divisions (Dodds and Pittendrigh, 1946 ; Dodds and Simmonds, 1946).

Many new clones have since been added to the Imperial College collection and the taxonomic relationships of the cultivars have been elucidated (Simmonds and Shepherd, 1956). Only two wild species, *M. acuminata* and *M. balbisiana*, seem to be involved in the evolution of edible bananas and their relative contributions to each cultivar can be simply defined by a genome formula. This knowledge renewed interest in comparing clonal behaviours in crosses with these two species.

Earlier work on the clone Gros Michel (Shepherd, 1954) revealed two unexpected features of seed-distribution within the fruit bunch : first, that basal "hands" of fruit were much more fertile than apical ones ; second, that seeds were limited to the apical half of the individual fruit. As far as possible these factors have been analysed in the current survey.

In Gros Michel it was found that the time of day of pollination affected fertility. Experiments are now recorded on several other clones and on a greater range of pollination times.

Materials and methods.

The edible clones used and their origins were as follows, A indicating a chromosome set from *M. acuminata*, B a set from *M. balbisiana* :

1. Diploid (AA) : Tongat (Type 33), Sikuzani (Type 38), Paka (Type 39) and J.349. The last is a weakly parthenocarpic diploid of the parentage Highgate × *M. acuminata*, Highgate being a somatic mutant of Gros Michel (Wilson, 1946).

2. Triploid (AAA) : Gros Michel (Type 1), Red (Type 34), Lujugira (Type 44), Kitarasa (Type 46).

3. Triploid (AAB) : Mysore (Type 6), Pome (Type 15), Horn Plantain (Type 23), French Plantain (Type 24), Rajapuri (Type 26), Nadan (Type 29), Nendra Padaththi (Type 30), Grindy (Type 35), Sept-Semaines (Type 36).

4. Triploid (ABB) : Bluggoe (Type 11), Awak Legor = Pisang Awak (Type 12), Peyan (Type 27), Ney Mannan (Type 28), Pacha Bontha Bathees (Type 31), Nyeupe (Type 55).

5. Tetraploid (ABBB) : Tiparot = Klue Teparod (Type 37).

For the most part, the pollens used were from the following clones of diploid wild species : *Musa acuminata* subsp. *malaccensis* (IR 53, clone Selangor of previous publications) ; *M. acuminata* subsp. *burmannica* (IR 124, clone Calcutta 4) ; and *M. balbisiana* (IR 100, clone Ceylon) (*M. acuminata* subspecies after Simmonds, 1956). In subsidiary experiments on Gros Michel and on diploid (AA) cultivars, pollen was taken from various wild strains, diploid cultivars and interclonal hybrids of *M. acuminata*.

The method used for pollination experiments was a simplified version of that evolved by Dodds and Simmonds (Simmonds, 1952). Separate nodal clusters (hands) were treated as blocks and the pollens or time treatments used were assigned at random to equal sections of each hand. Hence variation between bunches of fruit and between hands on a bunch was eliminated from the main comparisons. Pollen was applied in paper-lined plasticine cups pinched over the stigmas. Normally, pollinations were done during the morning of flower opening. Fruit was searched when ripe and seeds were recorded in most cases for four equal portions of the placental length, Zone I being apical, Zone IV basal. Seeds were classified as " good " or " bad " on their appearance, density, hardness and endosperm content but the low viability of even the " good " seeds indicates that this discrimination is arbitrary.

Statistical analysis of yields, where attempted, has been based on the sum of "good" and "bad" seeds in each "plot". Plots rarely contained more than four fruits, a limitation imposed by the material, and plot yields were consequently low in many experiments. Following Simmonds (1952), the transformation $\sqrt{(x+0{\cdot}5)}$ was used in analysis for all but the highest-yielding clones.

Chromosome counts of seedlings were made from root-tip squashes by the oxyquinoline-orcein method of Tjio and Levan (1950). Chromosome numbers of some of the Tiparot progeny were estimated only from stomatal size and frequency (Simmonds, 1948).

RESULTS.

Seed yields.

Seven clones yielded no seeds at all. These, with the number of fruits pollinated in each, were : Lujugira (186), Kitarasa (39), Horn Plantain (81), French Plantain (150), Rajapuri (525), Nadan (828) and Nendra Padaththi (132). Yields from the remaining clones are summarized in Tables I and II. General conclusions to be drawn are :

1. Triploids of genomic constitution AAA or AAB are usually infertile or scarcely fertile, whereas those of constitution ABB are usually appreciably fertile. It should be noted that the latter have about 500 ovules per ovary, the former classes about 200, but the relative difference in fertility is of much greater magnitude.

2. Pollen of *M. balbisiana* is more or less totally ineffective on edible clones of *M. acuminata* (AA and AAA) although the cross between the wild species is readily achieved.

3. As the contribution of *M. balbisiana* to the clonal genotype increases, so does the relative fertility of the *M. balbisiana* cross, but this only equals or exceeds the *M. acuminata* crosses in one case, Tiparot, where the former species contributes three of the four genomes present.

4. In three instances *M. acuminata* subsp. *burmannica* is clearly and unexpectedly

TABLE I.

Seed yields of relatively fertile clones.

Chromosome complement	Clone (female)	No. of experiments	Fruits per treatment	"Good" and "bad" seeds per fruit with pollen of: *malaccensis* (Aml)	*burmannica* (Abr)	*balbisiana* (B)	Conclusions
AA	J.349	4	134	18·06+5·93	26·98+2·60	0 +0·02	Abr > Aml > B
		2	73	7·93+5·93	—	0 +0·60	
AAA	Red	6	108†	0·47+3·39	0·38+3·21	0 +0·08	Abr=Aml >B‡
		3*	49	0·31+2·45	—	0 +0·02	
ABB	Awak Legor	2	36	13·22+7·53	12·39+5·58	7·28+5·33	Abr=Aml > B
		4	85	8·68+8·05	—	6·19+5·47	
	Nyeupe	1	25	1·64+0·32	0·80+0·28	0·64+0·24	Aml > B (?)
		2	66	0·82+0·21	—	0·53+0·21	
	Bluggoe	7*	98	1·90+0·35	2·67+1·70	0·11+0·44	Abr > Aml > B
	Ney Mannan	5	115†	4·88+2·23	7·64+6·06	0·40+3·05	Abr > Aml > B
ABBB	Tiparot	2	34	6·79+1·56	10·85+2·94	9·56+3·50	B = Abr > Aml ‡
		3	58	1·90+0·84	—	3·84+3·91	

* One infertile experiment excluded.
† Fertility with *M. balbisiana* based on a smaller number of fruits.
‡ Great variation between experiments.

TABLE II.

Seed yields of infertile clones.

Chromosome complement	Clone (female)	No. of experiments	Fruits per treatment	Total "good" and "bad" seeds with pollen of: *malaccensis*	*burmannica*	*balbisiana*
AAA	Orotava	9	196	6+10	11+4	0
	Palimbang ..	8	126	0+4	0+3	0
	Rio	8	132	5+9	9+7	0
AAB	Mysore	14	720	9+53	10+27	3+18
	Pome	8	171	9+3	6+7	1+0
	Grindy	1	20	1+5	—	0
	Sept-Semaines ..	2*	39	0	2+0	0
ABB	Peyan	1	44	0+1	—	0
	Pacha Bontha Bathees ..	9	276	4+2	7+3	0

* Two other experiments, with *malaccensis* and *balbisiana* only, yielded no seeds at all.

a superior pollen parent to subsp. *malaccensis*. This is most remarkable on J.349 which, phenotypically, is very close to subsp. *malaccensis* ; yet seeds set with subsp. *burmannica* are both more numerous and more frequently " good ". In the case of Ney Mannan, at least, the yield difference is more than compensated by differential germination of the " good " seeds from the two crosses (see Table X). Pollination

with subsp. *malaccensis* yields roughly half as many total seeds, which are more than twice as viable.

5. Female fertility may be altered by somatic mutation which possibly includes structural change in the chromosome complement. The clones Awak Legor and Nyeupe are identical in appearance, yet the latter is conspicuously less fertile. Nadan differs from Pome only in its larger and more blunt-tipped fruits, so that the origin of the one from the other by somatic mutation is likely. But Pome is slightly fertile, Nadan not at all.

Time of pollination.

A preliminary series of experiments on two clones followed the pattern of those on Gros Michel (Shepherd, 1954) in that comparison was limited to morning and afternoon pollinations on the day of flower opening (T_2 and T_3 of Table III). In J.349, morning pollination was much superior ; in Bluggoe there was no significant difference.

TABLE III.

Time of pollination.

Clone and pollen	No. of experiments	Fruits per treatment	Total seeds per fruit at times:*				Conclusions
			T_1	T_2	T_3	T_4	
J.349 × *malaccensis* ..	1	43	—	22·58	7·12	—	$T_2 > T_3$
Bluggoe × *malaccensis* ..	5	105	—	1·79	1·47	—	Not significant
Malaccensis selfed ..	2	28	62·25	55·57	38·21	10·57	$T_1 = T_2 > T_3 > T_4$
Burmannica selfed ..	2	32	64·84	67·19	65·72	59·22	$T_1 = T_2 = T_3 > T_4$‡
Red × *burmannica* ..	5†	39	8·03	3·27	2·49	—	$T_1 > T_2 = T_3$
		36	—	4·08	3·78	1·83	$T_2 = T_3 > T_4$
Bluggoe × *burmannica* ..	6†	63	3·81	1·98	2·08	—	$T_1 > T_2 = T_3$
		36	—	2·14	2·64	0·67	$T_2 = T_3 > T_4$
Nan Mannan × *burmannica*	6	117	19·79	22·45	19·31	10·57	$T_2 > T_1 = T_3 > T_4$
Awak Legor × *burmannica*	4	45	16·78	15·07	12·44	3·22	$T_1 = T_2 > T_3 > T_4$

* T_1, afternoon of day preceding receptivity; T_2, morning of day of receptivity; T_3, afternoon of day of receptivity; T_4, morning of day after receptivity.

† Red and Bluggoe have rather few fruits per hand, often too few to include four treatments. In some cases T_1 was omitted because flower opening was not anticipated correctly.

‡ Interaction between treatments and experiments was also significant.

Further experiments on the more fertile triploids and on two wild diploids showed clearly that this is an effect of age of flower. The comparison was extended to include pollinations on the afternoon previous to flower opening (T_1) and of old flowers on the morning of the day after flower opening (T_4). As Table III shows, late pollinations always resulted in lower yields. A more interesting discovery is that in two of the four triploids, Red and Bluggoe, pre-receptive pollination gave significantly more seeds and only in Ney Mannan were they significantly less.

This might have been a most important practical result for banana breeding where the low fertility of Gros Michel is a limiting factor. However, in a subsequent trial on this clone, 106 bunches pollinated before receptivity (T_1) averaged 0·74 seeds each, while 126 pollinated at receptivity (T_2) averaged 1·58. Other recent trials on

Gros Michel indicated that the optimum pollination time here is probably late rather than early morning on the day of receptivity.

However, some practical advantage may be derived in the case of parthenocarpic diploids, in which female fertility is becoming increasingly important to the banana breeder. Table IV summarizes the results of T_1 and T_2 pollinations compared in miscellaneous crosses of three diploid (AA) cultivars. In each case about twice as many total seeds were obtained from the earlier pollinations although the increase in " good " seeds was of a lower order.

TABLE IV.

Time of pollination.

Clone	Number of fruits		" Good " and " bad " seeds per 100 fruits	
	T_1*	T_2*	T_1	T_2
Tongat	238	253	7·1+47·9	4·7+18·6
Sikuzani	212	212	38·2+67·9	19·8+23·6
Paka	279	297	9·7+10·8	7·4+3·4

* T_1 and T_2, as in Table III.

Effect of hand order on fertility.

In a sample of 500 fruit bunches of Gros Michel averaging about eight hands each, more than half of the seeds were found in the two basal hands (Shepherd, 1954). Some comparable data for six other clones are given in Table V. The means are

TABLE V.

Effect of hand order on fertility.

Clone and pollen	No. of experiments	Mean seeds per fruit in hand :								
		1 (basal)	2	3	4	5	6	7	8	9 (apical)
J.349 × *malaccensis* ..	3	16·6	20·5	26·4	23·5	23·2	12·9	12·6	18·4	20·6
J.349 × *burmannica* ..	2	35·3	28·4	38·2	31·1	31·2	22·4	22·4	29·0	20·5
Red × *acuminata** ..	12	2·4	4·3	3·8	3·5	—	—	—	—	—
Awak Legor × *acuminata**	4	22·2	22·2	17·0	17·6	15·5	14·8	—	—	—
Awak Legor × *balbisiana*	3	21·4	18·7	11·7	11·0	7·5	8·3	—	—	—
Bluggoe × *malaccensis* ..	11	0·8	1·4	1·5	3·2	—	—	—	—	—
Bluggoe × *burmannica* ..	9	3·1	3·2	3·6	4·2	—	—	—	—	—
Ney Mannan × *malaccensis*	3	6·0	7·2	6·4	5·4	4·0	—	—	—	—
Ney Mannan × *burmannica*	5	18·9	21·7	18·1	20·5	20·2	14·6	—	—	—
Tiparot × *balbisiana* ..	3	7·4	5·6	10·9	11·3	9·3	—	—	—	—

* *malaccensis* and *burmannica* combined, since yields with these pollens are equivalent (see Table I).

derived from the means within hands rather than from the hand totals of separate experiments. The use of totals, based on varying numbers of fruits, would have given excessive weight to a few experiments.

It is clear that the striking fertility gradient of Gros Michel is not a general feature of edible clones, although there is a suggestion that Awak Legor behaves similarly. On the other hand it is possible that a contrary gradient exists in Bluggoe, the last hand being the most fertile.

Location of seeds within fruits.

Seeds in Gros Michel have previously been found to be virtually restricted to the apical (stylar) half of the fruit (Shepherd, 1954). Table VI compares the distributions of seeds in the fruits of eight other fertile clones in various crosses. The few seeds recovered from less fertile clones reveal similar trends. It will be seen that apical bias of seeds is a general phenomenon in edible bananas but in no other triploid is it as marked as in Gros Michel. The greatest concentration of seeds may be in the first or second quarter from the stylar end.

TABLE VI.

Distribution of seeds within fruits.

Clone and pollen	No. of fruits	Percentages in zones :*			
		I	II	III	IV
Gros Michel × Pisang Lilin†	868	86·1	13·7	0·2	0
J.349 × *malaccensis*	2,550	37·8	33·4	23·2	5·6
J.349 × *burmannica*	3,374	31·3	30·8	26·1	11·8
Tongat × *burmannica*	206	53·6	41·3	5·1	0
Red × *malaccensis*	417	58·0	35·7	5·8	0·5
Red × *burmannica*	388	53·6	40·5	5·4	0·5
Awak Legor × *malaccensis*	747	36·9	40·6	20·9	1·6
Awak Legor × *burmannica*	647	33·8	38·8	22·6	4·8
Awak Legor × *balbisiana*	454	36·6	41·4	20·0	2·0
Nyeupe × *malaccensis*	117	54·7	33·3	12·0	0
Nyeupe × *burmannica*	71	57·7	33·8	8·5	0
Bluggoe × *malaccensis*	220	23·2	43·6	31·8	1·4
Bluggoe × *burmannica*	421	24·5	43·7	29·7	2·1
Bluggoe × *balbisiana*	54	24·1	63·0	13·0	0
Ney Mannan × *malaccensis*	817	21·1	37·1	30·2	11·6
Ney Mannan × *burmannica*	1,554	23·0	33·5	30·1	13·4
Ney Mannan × *balbisiana*	275	25·8	44·4	28·4	1·5
Tiparot × *malaccensis*	351	38·5	35·6	21·9	4·0
Tiparot × *burmannica*	479	31·3	38·0	23·8	6·9
Tiparot × *balbisiana*	503	30·0	33·8	28·0	8·2

* Zones are equal portions of the placental region ; zone I is the apical end, zone IV the basal.
† Data from Shepherd (1954).

Differences between the pollen parents are evident, the least bias being usually in the cross with *M. acuminata* subsp. *burmannica*. Such differences commonly show an inverse relation to the fertility of the cross, but not in Awak Legor.

The inverse relation between fruit fertility and apical bias is usually apparent within crosses also, as is illustrated for J.349 in Fig. 1. For each experimental plot the percentage of seeds in the basal half of the fruit has been plotted against the mean seeds per fruit. Relationships are approximately linear and the following regressions for positions on yields have been calculated (23 pairs of observations for each pollen):

× *malaccensis* :	$b = 0{\cdot}898 \pm 0{\cdot}187$ % per seed ;
× *burmannica* :	$b = 0{\cdot}552 \pm 0{\cdot}196$ % per seed ;
Joint regression :	$b = 0{\cdot}838 \pm 0{\cdot}139$ % per seed.

The difference between the regressions for separate pollens is not significant. Further, an analysis of covariance shows that the percentages in the basal half, corrected for this regression, are still significantly different for the two pollens ($t_{43} = 2{\cdot}96$).

A similar correlation probably exists in Red, Awak Legor and Tiparot but it is obscured by low yields in the first, or by excessive error variance. At the other

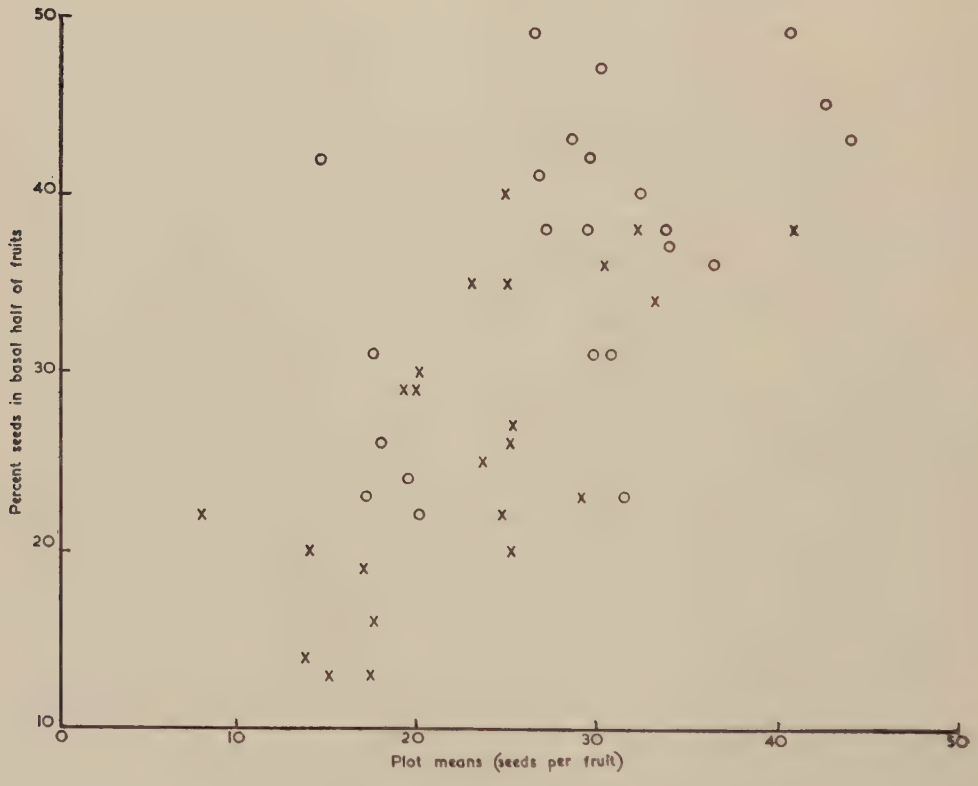

Fig. 1.

" Plot " fertility and seed distribution in J.349.
X, *malaccensis* pollen ; o, *burmannica* pollen.

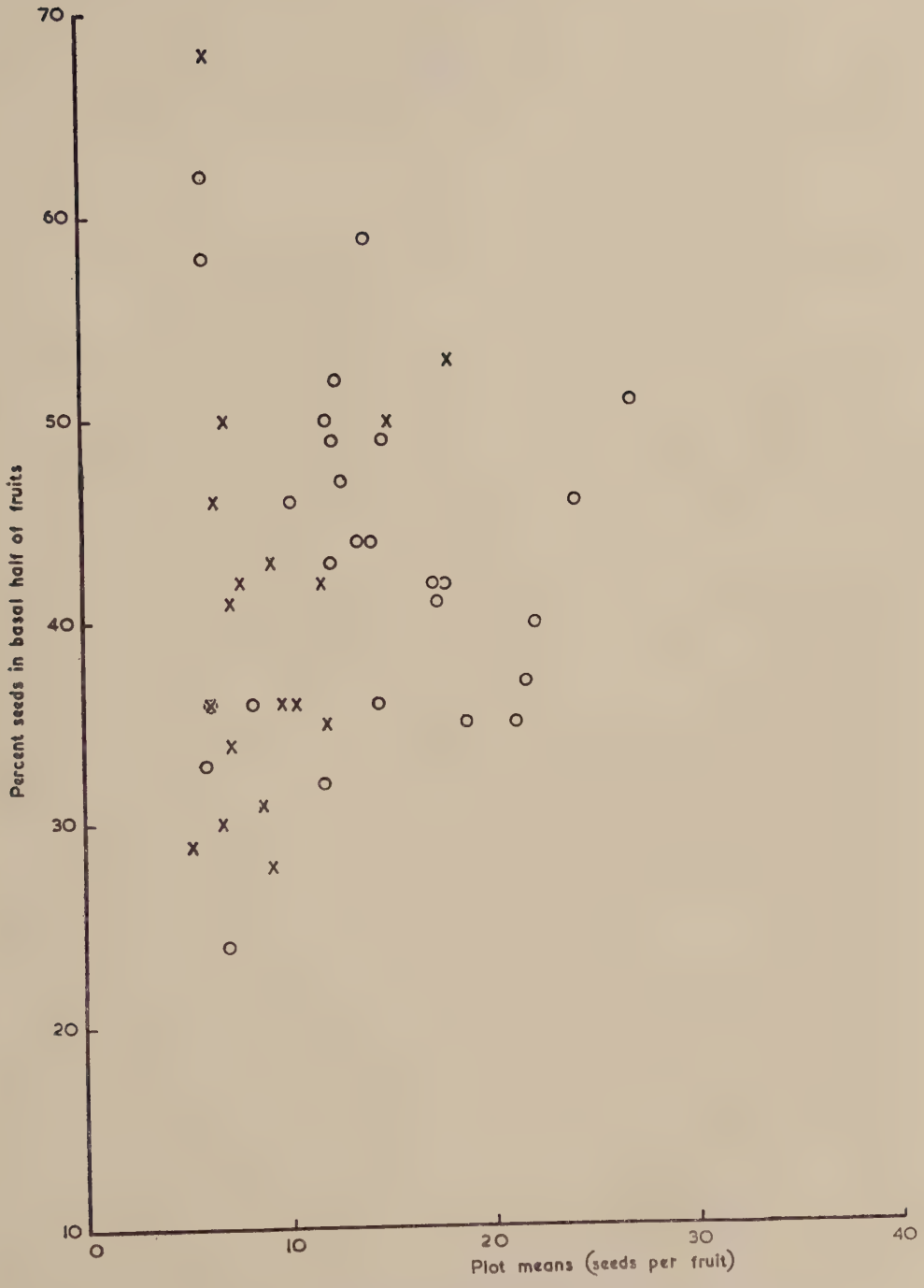

FIG. 2.

" Plot " fertility and seed distribution in Ney Mannan.
X, *malaccensis* pollen ; o, *burmannica* pollen.

extreme it is apparent that seed location is independent of fertility in Ney Mannan (Fig. 2), and probably also in Bluggoe though yields here are too low for confident assessment. The trends are further illustrated in Table VII, where separate fruits of each cross have been classified in arbitrary fertility levels and the proportions of distal seeds in the class totals are compared.

TABLE VII.

Individual fruit fertility and location of seeds.

Clone and pollen	Percentage of seeds in distal half of fruits with total seeds :					
	1-10	11-20	21-30	31-40	41-50	51-60
J.349 × *malaccensis*	—	82	71	68	61	—
J.349 × *burmannica*	—	70	68	61	56	55
Red × *acuminata*†	98	84	—	—	—	—
Awak Legor × *malaccensis*	90*	84	79	74	—	—
Awak Legor × *burmannica*	—	71	74	68*	—	—
Awak Legor × *balbisiana*	89	82	73	65*	—	—
Bluggoe × *burmannica*	65*	73	—	—	—	—
Ney Mannan × *malaccensis*	60	56	—	—	—	—
Ney Mannan × *burmannica*	60	56	56	—	—	—
Tiparot × *malaccensis*	84*	72*	69*	—	—	—
Tiparot × *burmannica*	—	68*	70	—	—	—
Tiparot × *balbisiana*	75*	63	60	—	—	—

* Categories with less than 200 seeds but more than 100 ; those with less than 100 seeds have been excluded.

† *malaccensis* and *burmannica* combined.

In some cases time of pollination also affects the distribution of seeds within fruits (Tables VIII and IX). In *M. acuminata* subsp. *malaccensis*, in Tongat,

TABLE VIII.

Seed distributions from different pollination times.

Clone and pollen	Percentage of seeds in distal half of fruits pollinated at :*			
	T_1	T_2	T_3	T_4
Malaccensis selfed	53·0	56·6	58·1	70·3
Burmannica selfed	45·8	47·9	48·1	51·0
Bluggoe × *malaccensis*	—	68·6	76·6	—
Bluggoe × *burmannica*	65·8	68·2	69·7	—
Ney Mannan × *burmannica*	59·0	57·0	58·7	—
Awak Legor × *burmannica*	75·7	74·2	73·9	—

* Times T_1, etc., as in Table III.

TABLE IX.

Seed distributions from different pollination times.

Clone	Percentage of seeds in distal quarter of fruits pollinated at :*		
	T_1	T_2	T_3
Tongat	38·5	71·7	—
Sikuzani	83·1	91·9	—
Paka	60·9	63·6	—
Gros Michel	64·1	66·3	—
Red	42·8	51·8	60·4

* Times T_1, etc., as in Table III.

Sikuzani, Red and Bluggoe, earlier pollination is associated with a less restricted distribution. All are clones in which earlier pollination also results in greater fertility and some of this enhanced fertility can certainly be attributed to more efficient fertilization in relatively basal parts of the ovary.

Pollen tube growth.

Failure of pollen tubes has been observed in Gros Michel (Shepherd, 1954) and in Dwarf Cavendish (G. B. Wilson, unpublished). Pollen tube growth has now been examined in the styles of a wide range of clones and at least two types of failure occur. The more common is that morphological or physiological immaturity of the stigma (or style) may prevent or delay the penetration of tubes. This is most conspicuous in the Cavendish forms and in Tongat but occurs occasionally in most clones, if not in all. In Dwarf Cavendish whole inflorescences are often affected, the flowers as a whole being conspicuously immature and not opening normally. In other instances the discrepancy in timing between bract or flower opening and stigma receptivity is less than one day in magnitude. Pollination at flower opening does not then necessarily result in total failure of tube penetration ; sometimes a few tubes are present in these styles but they have not grown so far as tubes in normal styles after the same time. Pollination of other styles in the same hand one day or even a few hours later can induce quite normal tube growth.

The other type of failure arises from a barrier in the style itself, similar in effect to that imposed by oppositional alleles in other plants. Though penetration succeeds, whether delayed or not, all or some of the tubes are later impeded at different points in the style, not infrequently near the base, and their tips swell. Such behaviour has been seen rarely in Ney Mannan and Pacha Bontha Bathees, where it is apparently associated with old flowers ; more frequently in Palimbang and Mysore, where it is a feature of newly-open or immature flowers. In all cases the incidence within inflorescences is erratic and many inflorescences are unaffected.

Ploidy of progeny.

Table X includes the author's findings and those of Cheesman and Dodds (1942) where the latter are considered to be a useful supplement. There is slight disagreement in that the current records show a higher frequency of aneuploids.

TABLE X.

Germinations and seedling ploidy.

Clone and pollen	"Good" seeds sown	Germinated	2n							
			22	23-24	25-32	33	44	55	77	Total
Red × *malaccensis*	43	4	—	—	4	—	—	—	—	4
Red × *malaccensis**	720	45	4	—	6	1	—	—	—	11
Red × *burmannica*	152	14	1	2	6	—	—	—	—	9
Red × *burmannica**	534	59	3	1	—	1	—	—	—	5
Awak Legor × *malaccensis*	100	4	—	—	—	—	—	—	2	2
Awak Legor × *malaccensis**	365	25	—	—	—	—	7	—	18	25†
Awak Legor × *balbisiana*	100	31	—	—	—	—	24	—	1	25
Nyeupe × *malaccensis*	41	8	—	—	—	—	3	—	—	3
Nyeupe × *burmannica*	19	1	—	—	—	—	1	—	—	1
Nyeupe × *balbisiana*	15	4	—	—	—	—	3	—	—	3
Bluggoe × *malaccensis*	299	54	20	10	1	—	1	—	—	32‡
Bluggoe × *malaccensis**	237	31+	4	—	—	—	2	—	—	6
Bluggoe × *burmannica*	15	6	3	3	—	—	—	—	—	6
Bluggoe × *burmannica**	305	11	—	2	—	—	—	—	—	2
Bluggoe × *balbisiana*	10	2	—	—	—	2	—	—	—	2
Bluggoe × *balbisiana**	97	8	—	—	—	1	2	—	—	3
Ney Mannan × *malaccensis*	440	116	29	47	18	1	2	—	5	102
Ney Mannan × *burmannica*	649	94	20	31	15	—	—	1	1	68
Ney Mannan × *balbisiana*	99	22	2	1	3	3	4	—	5	18
Tiparot × *malaccensis*	50	10	—	—	—	5	—	2	—	7
Tiparot × *balbisiana*	50	12	—	—	1	5	—	4	—	10

* Cheesman and Dodds (1942).
† Only four seedlings counted; ploidy of others inferred from the authors' comments in the text.
‡ Many seedlings were very weak and died before counts could be made.

Two contrasting behaviours are evident in the triploids :

1. In Awak Legor and Nyeupe only unreduced and double restitution gametes yield viable seeds. The rarity of heptaploids in Awak Legor × *M. balbisiana* is noteworthy.

2. In Red, Bluggoe and Ney Mannan successful embryo-sacs are at least predominantly the products of irregular meiosis. It is clear, even from very low numbers, that zygotic survival is low for diploids and aneuploids of the *M. balbisiana* cross (see discussion).

The presence of functional unreduced embryo-sacs (yielding pentaploids) in the tetraploid Tiparot is of interest. One case of a functional hypodiploid spore is also noted (bottom line of Table X).

DISCUSSION.

So far as has been observed (Dodds, 1945 ; Shepherd, 1954 ; Simmonds, unpublished), the frequency of normal embryo-sacs in ovules of edible clones is low, for largely obvious reasons. Diploid cultivars are generally heterozygous for at least

one translocation and inversion bridges are also found (Dodds, 1943 ; Shepherd, unpublished). Sikuzani is exceptional in being structurally homozygous but there is some failure of pairing in pollen mother cells. Apart from meiotic errors, Dodds (1945) reports a high incidence of multiple archesporia in the diploid cultivar Pisang Lilin (Type 32), with consequent failure of embryo-sac formation.

In triploids a gross disturbance of gametogenesis is to be expected, giving rise generally to unbalanced aneuploid spores. That these may yield functional embryo-sacs is evident in Red, Bluggoe and Ney Mannan from the ploidy of their progeny. Trivalent frequencies are low in pollen mother cells of Bluggoe and Ney Mannan (Shepherd, unpublished) and presumably also in megaspore mother cells. Many univalents are excluded from the daughter nuclei and the likelihood of haploid or near-haploid gametes is therefore increased. Further, since in these ABB hybrids the excluded chromosomes are probably those of the *M. acuminata* genome, the haploids and low aneuploids should approximate more or less closely to a balanced genome of *M. balbisiana*. In an analogous case, a diploid seedling derived from Pome (AAB) $\times$*M. acuminata* was found to have no recognizable feature of *M. balbisiana* in its phenotype : the B genome of the triploid parent was totally lost.

The species components of diploid, trisomic and low aneuploid progeny of Bluggoe and Ney Mannan $\times$*balbisiana* could probably be assessed with some certainty if they could be raised in sufficient numbers. They might further provide information on linkage in *M. acuminata* since in some cases single chromosomes or parts of chromosomes of this species would be isolated against a background of the other. Paradoxically, however, such progeny are rarely recovered and are never vigorous, while the combination of virtually *M. balbisiana* egg cells and *M. acuminata* male nuclei yields many vigorous diploids and trisomics.

Red, Bluggoe and Ney Mannan also yield triploid progeny, from which the existence of diploid megaspores and embryo-sacs is inferred. These might result from a rare segregation at the first meiotic anaphase or from restitution at the second division. From the arguments above, such mechanisms in ABB hybrids would yield spores approximating respectively to an AB hybrid and to *M. balbisiana* (BB). One such triploid from Bluggoe $\times$*M. balbisiana* has been raised to flowering and its phenotype, while differing from that of Bluggoe, is that of an ABB hybrid. That is, the megaspore from which it was derived was diploid by segregation rather than by restitution.

Dodds and Simmonds (1946) have outlined the modes of restitution common in *Musa*. In diploid hybrid material, meiosis was sometimes omitted entirely, the chromosomes dividing within the resting nucleus to yield a tetraploid spore. In other cases, chromosomes condensed and pairing occurred but restitutions at both divisions, or at the second division only, led to tetraploid or diploid spores. In *M. acuminata* subsp. *burmannica*, the author has recently seen indications of a successful second division following first division restitution. The mechanisms of restitution are thus apparent, but the event, providing an escape from sterility, does not seem to be a common one in megasporocytes of cultivars except perhaps in Awak Legor.

Unreduced spores in the tetraploid Tiparot make the first such record for a tetraploid banana. Other (synthetic) tetraploids have been crossed previously but have behaved as functional diploids. Meiosis has been observed in pollen mother cells of a few tetraploids ; it is by no means regular. Hypodiploid spores, such as that

which yielded a 29-chromosome seedling from Tiparot, are probably frequent but rarely viable.

Embryo-sac failure obviously accounts for most of the sterility of edible clones, but it is evident also that fertility is further restricted by the genetic factors concerned with and associated with parthenocarpy, at least in some clones (Dodds, 1945 ; Dodds and Simmonds, 1948). Dodds recorded embryo-sacs in 2-33% of ovules in samples from four different naturally occurring diploid cultivars in which female sterility was virtually absolute. Shepherd (1954) found embryo-sacs in about 10% of Gros Michel ovules, whereas seed yields are from 0-0·2% of ovules. Simmonds (unpublished) found about 10% in Awak Legor, equivalent to the maximum seed fertility, and no mature embryo-sacs at receptivity in Bluggoe or Mysore. Bluggoe does in fact have occasional quite sterile bunches. The correspondence of embryo-sacs and seeds in Awak Legor, and the conclusion that ABB clones are inherently more fertile than triploids derived more from *M. acuminata*, support the inference that the genetic factors in the control of sterility are largely or wholly centred in the A genome.

The time of action of these genetic factors may be guessed at, although their mode of action is still obscure. Though seed failure may occur at all stages of parthenocarpic fruit development, the same is true of non-parthenocarpic forms; bad seeds are especially frequent in the clone of *M. acuminata* subsp. *burmannica* used in the present study. On the other hand Gros Michel only rarely yields an obviously bad seed ; almost all are hard and black though they do not necessarily germinate. It is thought, therefore, that the survival of a seed after fertilization is a matter of balance within the embryo, and between embryo and endosperm, and that it is relatively unaffected by the maternal environment of the developing fruit.

However, in the interval between pollination and fertilization there is definite evidence of aberrations peculiar to edible fruits. First, there are the abnormalities of pollen tube growth mentioned above. Such failures in the style might impose sterility on isolated fruits, though rarely more general sterility, but similar and perhaps more frequent failures to penetrate the ovary tissues are not unlikely. Dodds (1945) found that few pollen tubes did in fact reach the embryo-sacs of Pisang Lilin (Type 32) or those of certain derived diploid parthenocarpic seedlings (all AA), despite apparently normal tube growth in the styles. Moreover, of those pollen tubes which had penetrated an embryo-sac, the great majority were not functional, having failed to burst. This latter behaviour was confined to the parthenocarpic forms and was not found in a comparable survey of IR 53 (*M. acuminata* subsp. *malaccensis* of the present study) in which plant also the frequency of fertilization is often unaccountably low. Similar studies on a large number of clones would be useful though laborious, but it seems probable that failure of fertilization is the major factor in genetic sterility.

The question may also be raised : what distinguishes the internal environment of a sterile ovary from that of a fertile one, whether ultimately parthenocarpic or not? Simmonds (1953), in accounting for the early ovule growth commonly encountered in unpollinated parthenocarpic bananas, provides a possible clue in his suggestion that ovules in these fruits have either a greater hormone supply or an earlier one than those of seeded bananas. That parthenocarpy, sterility and hormone supply are interrelated is suggested by an experiment on Bluggoe, in which seeds were suppressed by the application of α naphthyl-acetic acid in lanolin to receptive ovaries (0·04 seeds

per fruit as against 1·25 in untreated fruits). Otherwise it has been observed in J.349, where the expression of parthenocarpy is variable, that strongly parthenocarpic hands or bunches are notably less fertile than the others. Conversely, certain hands or single fruits of Pome, Ney Mannan and Awak Legor are non-parthenocarpic but these are either sterile or much less fertile than their neighbours. Here, presumably, the factor lacking for parthenocarpy is also essential for seed development.

SUMMARY.

1. Female fertility is analysed for a wide range of banana cultivars, mainly triploid, of various origins.

2. Comparisons with pollen of two sub-species of *Musa acuminata* and of *M. balbisiana* reveal striking and sometimes unexpected differences in fertility, in distribution of seeds within fruits and in seedling ploidy.

3. A number of clones are shown to be more fertile when pollinated prior to flower opening.

4. The origins of viable embryo-sacs and the causes of sterility are discussed.

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THE GROWTH AND DEVELOPMENT OF EARLY SUMMER CAULIFLOWER IN RELATION TO ENVIRONMENTAL FACTORS

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It has been demonstrated by several workers that many crops show different responses to changes in soil moisture conditions at different physiological growth stages. As part of an investigation into the response of the early summer cauliflower (*Brassica oleracea* var. *botrytis* L.) to different soil moisture conditions at various growth stages, an analysis of the growth and development of the plant was made during 1957 and 1958 to provide information on the pattern of growth of the various organs. Particular attention was paid to the growth of the curd, a peculiar inflorescence which has been variously described as " monstrous ", " malformed ", and " hypertrophic ". Dark (1938) found that it was hypertrophied, but the flowers are not defective, the curd being a preliminary stage before the development of the flowers. Aamlid (1952) has reviewed the few papers published dealing with the morphology of the curd and his work has shown that the latter consists of a large number of naked apices of peduncles each surrounded by one or more whorls of indeterminate structures which develop either into apices of a new order of peduncles or into flowers.

Although the effects of environmental conditions on curd initiation and curd size have been studied by several workers (e.g. Aamlid, 1952 ; Parkinson, 1952 ; Jensma, 1957), little work has been published describing the growth of the curd under either controlled or field conditions.

A quantitative comparison of plant growth from year to year under field conditions is normally difficult because of the effects of variable climatic conditions. Thus, when the increase in weight of a plant is plotted against a normal time scale such as number of days from sowing, the resultant curves for plants subjected to the same experimental treatments can differ markedly from year to year. The author and several other workers at the National Vegetable Research Station have attempted to overcome this difficulty by the use of cumulative measurements of the main climatic variables as " time " scales, thereby providing a common time scale from year to year and also obtaining information on the most important climatic variables influencing growth. A general account of this work is given elsewhere (Nelder *et al.*, 1960). This paper describes the use of two of these " time " scales, accumulated temperature and accumulated solar radiation, which are relevant to the growth and development of the early summer cauliflower plant.

Materials and methods.

Plant material.

In both years plants of the variety Finney's 110 were grown at Wellesbourne under conditions comparable with normal commercial practice. Seed was sown

in cold frames in late September and the seedlings were pricked off into pots and over-wintered in frames until they were planted in the field the following March. A planting distance of 3 ft. × 2 ft., together with a progressive and even removal of plants during sampling, allowed ample room for growth, to avoid any possibility of competition between plants. The plants were irrigated sufficiently frequently (Salter, 1959) to prevent any depression of growth rate as a result of soil moisture stress.

Growth measurements.

Random samples, each of ten plants, were taken at intervals from the cotyledon stage (October) until the curd initials were visible (April-May). The numbers of leaves and leaf initials were counted after dissecting the growing points under a stereo-microscope at × 18 magnification and the fresh and dry weights of the whole plants were determined.

When five or more of the ten plants sampled had developed a wide apex indicative of the onset of curd development (Fig. 1, *b*) a more detailed analysis of the growth was begun. For this, samples of forty plants were taken at weekly intervals. In 1957 the mean fresh and dry weights of the plants were obtained, including as many roots as could easily be removed from the soil. The curds were measured and the sums per plant of the products of leaf length (including the petiole) and breadth were recorded. In 1958 the fresh and dry weights of the roots, stem, leaves and curd were measured separately. Up to mid-June in both years the dry-weight determinations were made on the entire sample of forty plants, but after this time a random sub-sample of ten plants was used. The plant material was dried at 100° C.

Meteorological measurements.

In the propagating frame, maximum and minimum temperatures during the previous 24 hours were recorded daily at 0900 hours G.M.T. In the field, similar daily maximum and minimum temperatures were obtained from the N.V.R.S. Agro-Met. Station situated about 100 yds. from the experimental plants. Accumulated day-degrees above various base temperatures were calculated from these records by the use of Meteorological Office Tables (1946). Solar radiation was measured by a Kipp thermopile.

Evaluation of the data.

It was desired to assess the rate of growth of the plants by methods that satisfied the following criteria: that they yielded growth curves which were of a recognizable mathematical form, and that the curves were comparable in two or more seasons. Accumulated measurements of the following environmental factors were tested as independent variables against which growth could be plotted: (I), day-degrees above a base temperature of 42° F. (5·6° C.); (II), solar radiation (gm. cal.); (III), the product of day-degrees and day-length; (IV), calculated evapo-transpiration; (V), evaporation from an open water surface. Of these, only the first (accumulated day-degrees) yielded results which satisfied the desired criteria in respect of all growth measurements and this will be dealt with in detail. The second factor (accumulated solar radiation) was also used for the assessment of leaf growth.

Fig. 1.

Early stages in the development of the cauliflower curd.

a. Normal vegetative apex.

b. Development of larger apex surrounded by leaf and bract initials.

c. Development of bracts.

d. Development of secondary meristems in the axils of the bracts.

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EXPERIMENTAL RESULTS.

Growth characteristics of the whole plant.

The increase in log dry weight of the plants, plotted against chronological time, is illustrated in Fig. 2. It is apparent that the curves are irregular and dissimilar in the

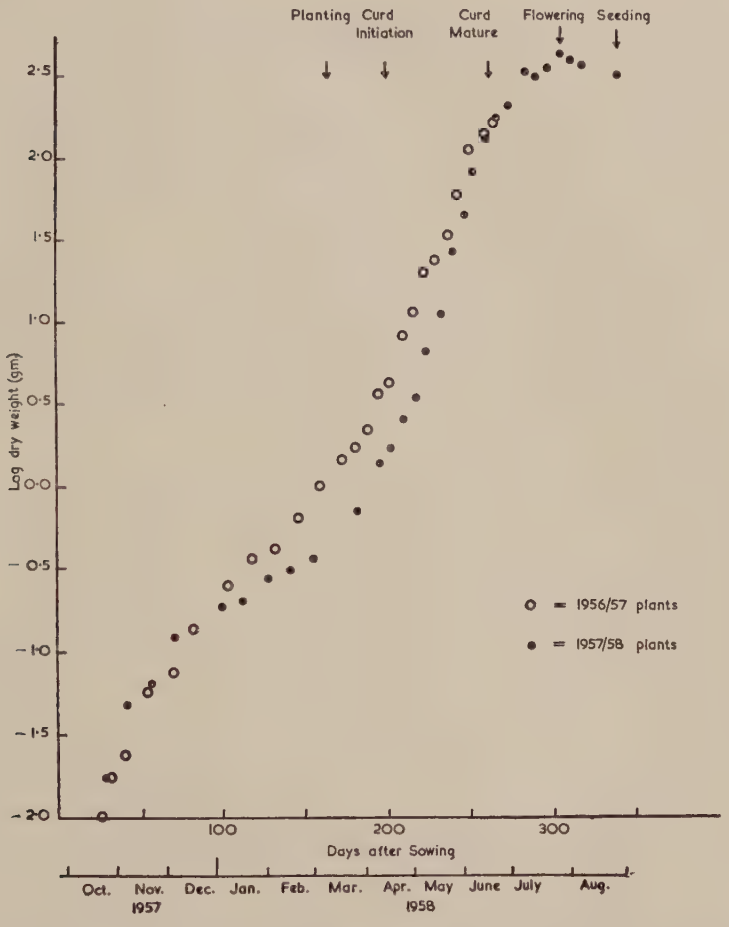

FIG. 2.

Growth curves of log total dry weight of plants for two years. The lower time scale is applicable to the plants grown from September 1957 until August 1958.

two seasons. Fig. 3 illustrates log dry weight plotted against accumulated day-degrees above a base temperature of 42° F. Growth is seen to be an exponential function of accumulated day-degrees and the two years' results are sufficiently similar to be adequately expressed by the same regression equations:

Frame conditions : $\log y = 0{\cdot}003030x - 2{\cdot}7331, \quad r = +0{\cdot}982$
Field conditions: $\log y = 0{\cdot}002698x - 2{\cdot}5567, \quad r = +0{\cdot}989$

where x = accumulated day-degrees above a base temperature of 42° F. and y = dry weight of the plant (gm.). The common regressions for the two years accounted for 96% and 97% of the variance under frame and field conditions respectively. Discontinuity between growth under frame and field conditions was caused by the check at planting time.

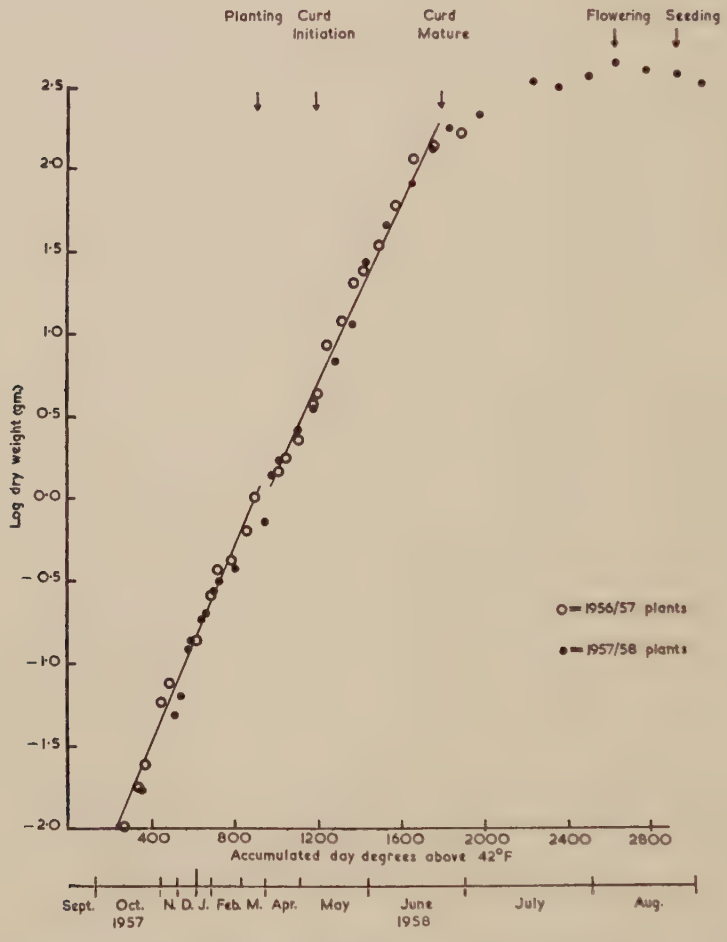

Fig. 3.

Growth curves of log total dry weight of plants for two years, using accumulated day-degrees above 42° F. as the common time scale. The lower time scale is applicable to the plants grown from September 1957 until August 1958.

In the calculation of day-degrees the use of 42° F. as a base temperature gave the most satisfactory results. A higher or lower base temperature increased the variance and reduced the correlation with growth.

The end of the period of exponential growth (Fig. 3) coincided in both years with the stage of curd maturity, i.e. just before the curd lost its compactness as a result of

the uneven growth of the individual branches of the inflorescence. This stage also coincided with the maximum leaf weight of the plant and, although the leaf weight afterwards became progressively smaller because of senescence of the leaves, the total weight of the plant continued to increase until flowering time when maximum dry weight was attained. Thereafter the plant weight became smaller until death occurred after seeding.

With this time scale the growth curve of the whole plant from germination until flowering time was approximately logistic in form and could be expressed in the form: $x = A/(1+be^{-kt})$, where x = dry weight, A = "final" dry weight, b is a constant, e = 2·718 (the base of the natural logarithms), k = initial relative growth rate and t = time. A linear relationship was obtained between growth and accumulated day-degrees over this period by the use of the linear form of the above equation, i.e. $\log (A-x)/x = \log b - kt$.

The growth curves for the total fresh weight for both years were similar to those for dry weight.

The use of accumulated gram-calories of solar radiation as a time scale against which to plot dry weight up to the time of curd maturity resulted in dissimilar curves for the two years. Nevertheless, as temperature and solar radiation are not independent of each other, a multiple regression analysis of dry weight on these two climatic variables was carried out, the main results of which are presented in Table I.

TABLE I.

Multiple regression analysis of dry weight on accumulated temperature and accumulated solar radiation.

	Sum of squares	Degrees of freedom	Mean square	F value
Mean regression on temperature (b'_1) ..	63·4093	1		
Mean regression on radiation after eliminating temperature	0·0025	1	0·0025	0·19 n.s.
Mean regression on radiation (b'_2)	60·8603	1		
Mean regression on temperature after eliminating radiation	2·5515	1	2·5515	191·84*
Mean regression on temperature and radiation	63·4118	2		
Difference of (b'_1) between years	0·0056	1	0·0056	0·42 n.s.
Difference of (b'_2) between years	0·4446	1	0·4446	33·43*
Remainder sum of squares within years ..	0·5333	40	0·0133	

* Level of significance: $P < 0·001$.

In both years the addition of solar radiation did not improve the fit to temperature, but the addition of temperature improved the fit to radiation. The sum of squares for difference of b'_1 in the two years was less than the mean error, while that for b'_2 was significantly different. The results of this analysis show that during 1957

and 1958 the growth of the cauliflower plant was more closely related to temperature than to solar radiation.

Initiation of leaves and curd.

The number of leaves of the sampled plants was plotted against accumulated day-degrees above the base temperature of 42° F. and a curvilinear relationship was found to persist until March, when approximately 20 leaves had been initiated. During this winter period, leaves continued to be initiated even when the temperature in the frame did not rise above 42° F. except for a short period each day. Consequently, base temperatures of 40, 38, 36, 34, 32, 30 and 28° F. were used from which

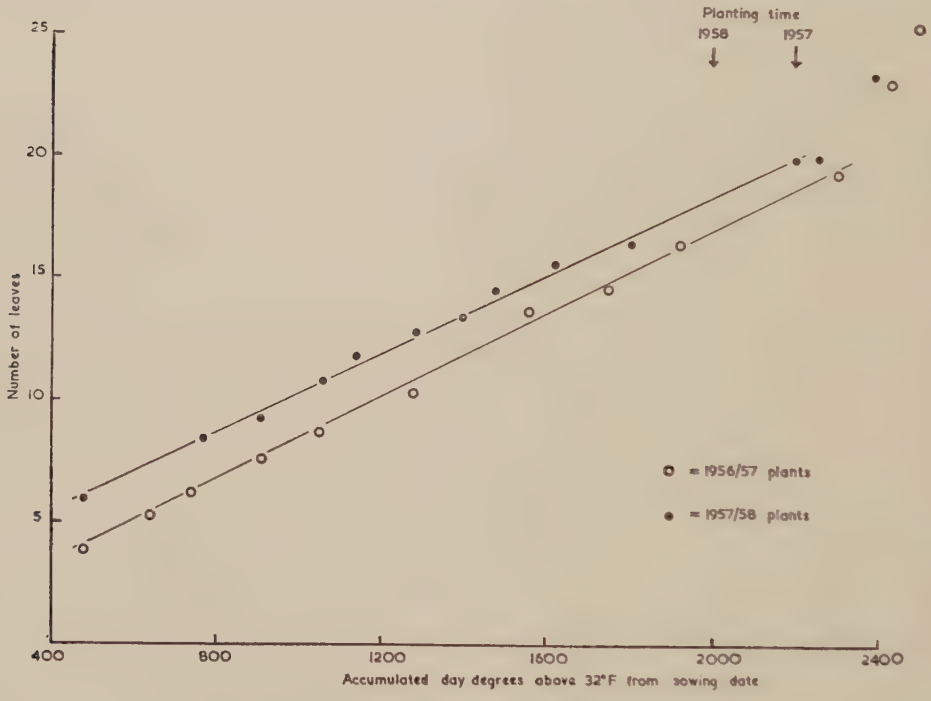

FIG. 4.

Number of leaves of cauliflower plants, related to accumulated day-degrees above 32° F. from sowing date.

to calculate day-degrees and it was found that, when leaf number was plotted against accumulated day-degrees above 32° F., a linear relationship, with the smallest error variance, was obtained until approximately 20 leaves had been formed (Fig. 4). Shortly after the 20-leaf stage of development it became difficult to differentiate between leaf initials and the initials of bracts which surrounded the apical dome during the transition stage between a vegetative and generative apex. As a result, the leaf number at this stage became subject to error and this would account for the high rate of " leaf " production observed during this period (Fig. 4). At a later stage of

development it was possible to differentiate between leaves and bracts when peduncles of the curd developed in the axils of the bracts.

Thus there is a suggestion that, in the cauliflower plant, leaf initiation occurs at temperatures too low for normal growth, as measured by increase in the dry weight of the plant.

There was a progressive change in the appearance of the stem apex associated with the initiation of the curd. Development of the curd started when about 20 leaves had been initiated and the normal apical dome was about 200μ in diameter (Fig. 1a). The dome widened to about 350μ and bracts were initiated (Fig. 1b), in the axils of which secondary meristems developed and formed the primary peduncles of the inflorescence (Fig. 1c). Further bracts and secondary peduncles grew on these (Fig. 1d) and in turn yielded further orders of peduncles. Aamlid (1952) observed fifth-order branches on a curd of marketable size and estimated that there were five million apices present at this stage.

Growth of curd.

When curd size, in terms of dry weight, fresh weight, mean diameter or volume was plotted against accumulated day-degrees, the curves obtained for both years until maturity were identical in form though slightly displaced relative to each other for the different years. The results presented in Fig. 5 indicate that the growth of the curd, in terms of dry weight, was related to accumulated temperature (Fig. 5(b) and (c)). The form of the relationship (Fig. 5(b)) was adequately fitted by the Gompertz curve (Winsor, 1932), log (A/W) = be^{-kt}, and the constant k had the same value, 0·029, for both years. This form of growth curve may have resulted partly from the use of accumulated temperature without correcting for supra-optimal temperatures and partly from the reduction of leaf weight which occurred during the period from curd maturity to flowering. Boswell and Jones (1941) have suggested that high temperatures may retard the growth of the curd and have shown that the cauliflower crop in the West of the United States reached maturity in the cooler half of the year when there were temperatures of 50-60° F. In the present investigation it was found that, when the log dry weight of the curd was plotted against accumulated temperatures between 42° F. and 55° F., the growth curve was almost logistic in form until maturity (Fig. 5(c)). Thus, up to this time, temperatures above 55° F. appeared to be partially responsible for the apparently declining growth rate. After maturity the gradual senescence of the leaves, with the resulting reduction in the supply of photosynthates to the curd, may possibly have contributed to the further decline in growth rate of the curd.

When the other " time " scales (not chronological time) were used, the growth curves for the two years were dissimilar. This is illustrated in Fig. 5(a) where the increase in dry weight of the curd for both years, 1957 and 1958, is plotted against accumulated solar radiation.

In 1957, when curd size until maturity was plotted against the number of days from sowing, an almost exponential curve was obtained irrespective of how the curd size was measured (Fig. 6). A similar result was obtained in 1958. Thus, with chronological time or accumulated day-degrees between 42° F. and 55° F. as the independent variable, similar growth curves were obtained. It was found that between each sampling date a similar number of day-degrees between 42° F. and 55° F.

had accumulated, resulting in a similar spacing of the experimental points and consequently giving similar growth curves.

Growth of leaves.

After initiation of the curd the increase in total dry weight of leaves was due to the growth of existing leaves and not to formation of new ones. The curve for increase

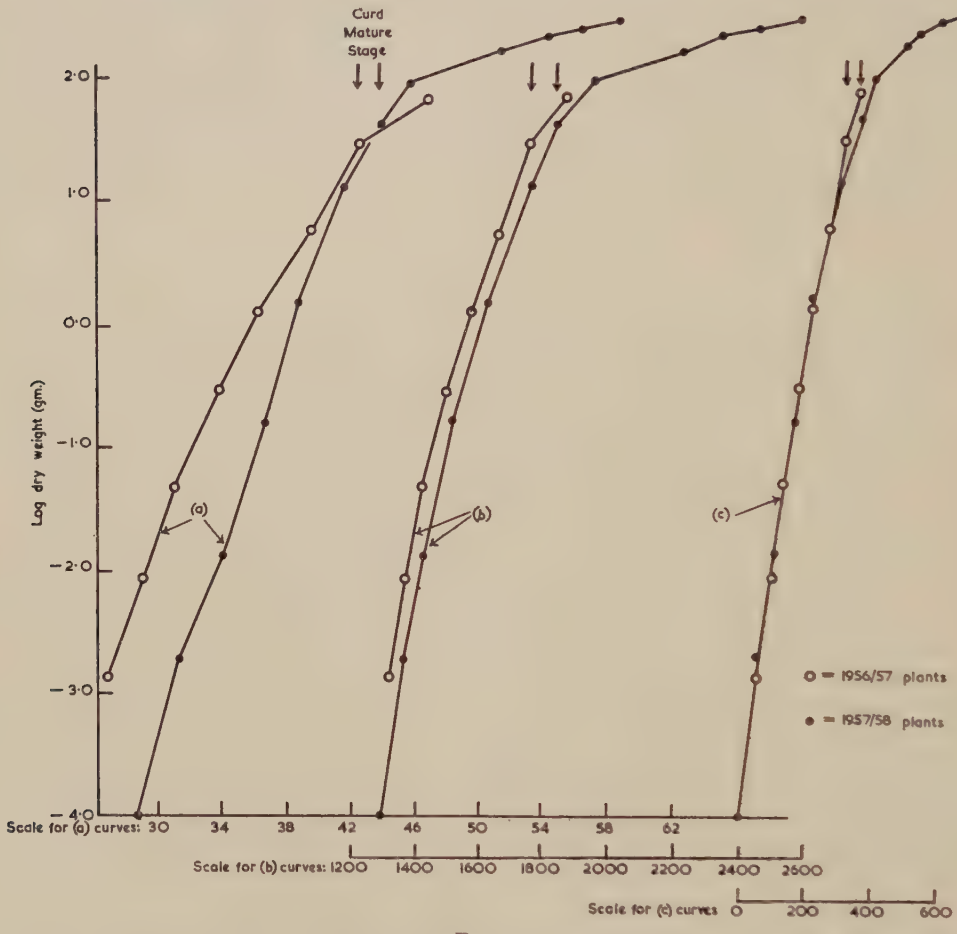

FIG. 5.

Growth curves of log curd dry weight resulting from the use of three different scales : (a) accumulated solar radiation from date of sowing (K. cal.) ; (b) accumulated day-degrees above 42° F. from date of sowing; (c) accumulated day-degrees between 42° F. and 55° F. from date of curd initiation.

in dry weight of the leaves from curd initiation to maturity in 1958 was logistic in form, whether accumulated day-degrees or accumulated solar radiation was used as the time scale. By the use of the linear form of the logistic equation, i.e. $\log (A-x)/x = \log b - kt$, a good fit was obtained between the growth of the leaves and either of the time scales. The regressions of growth on accumulated temperature and accumulated

solar radiation accounted for 97% and 99% of the variation respectively, assessed by the method of least squares.

A similar result was obtained in 1957 when the $\log_{10}$ of the sum of products of leaf dimensions was used as the criterion of leaf area (Salter, 1959). Thus in 1957 and 1958 leaf growth was closely related to temperature and solar radiation.

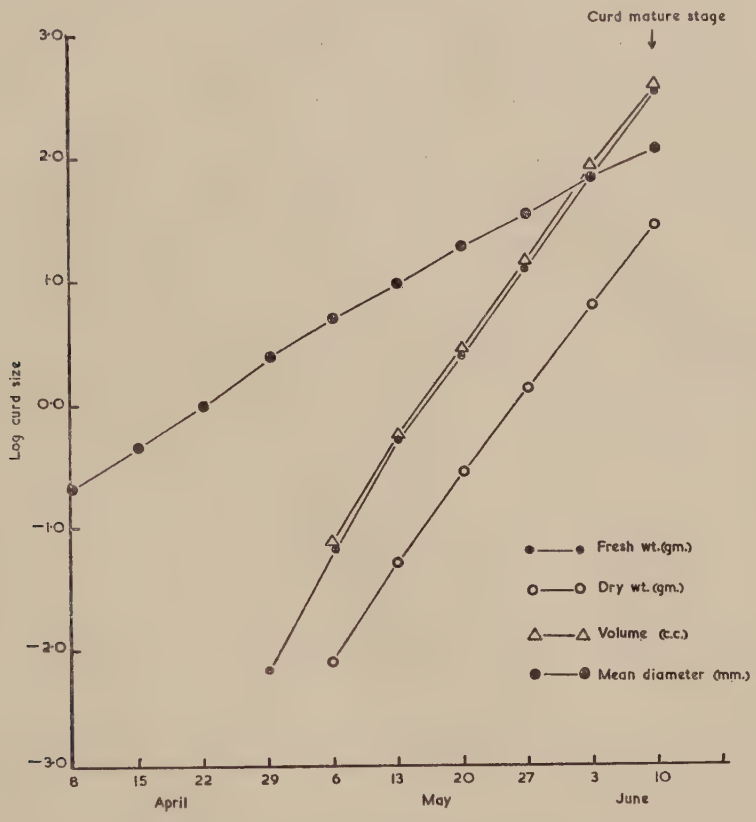

FIG. 6.
Increase in log curd size related to chronological time in 1957.

DISCUSSION.

By using climatic variables as " time " scales it was found that from seed sowing until curd maturity, when edaphic factors were non-limiting, growth of the cauliflower plant and its principal organs was more closely related to accumulated temperature than to any other climatic factor. In fact, the growth curve of plant dry weight for 1958 was almost coincident with that for 1957 when accumulated temperature was used as the " time " scale. Thus the use of accumulated temperature as the independent variable against which to plot growth has yielded growth curves of a recognizable mathematical form and enables a quantitative comparison of the growth curves to be made.

The concept that a plant requires a given number of heat units before maturity is reached was first suggested by Réaumur in 1735 (Abbe, 1905). It has been severely criticized by Went (1957) on the grounds that plant growth is not linearly related to temperature and that " . . . since heat is not a form of available energy for plants and only modifies other processes, it is logically impermissible to talk about, or even calculate, heat sums." Further criticisms of the use of accumulated temperatures are that the possible differential effects of night and day temperatures and the influence of temperature at different stages of growth are ignored. To overcome these criticisms of the concept of accumulated temperatures, various modifications have been tested, notably the " exponential indices " of Livingston and Livingston (1913). Nevertheless, many workers, e.g. Ottosson (1958), have correlated various stages in the development of a crop with accumulated temperature. Ottosson has carefully differentiated between *growth* and *development* in this connection and has stated " . . . when using the heat-unit system it should be borne in mind that the heat requirements apply to a certain phase of development and not to a given amount of growth". It is difficult to see why growth (i.e. increase in dry weight of the plant) has not been previously related to accumulated temperature when development (i.e. morphological changes not necessarily associated with increase in dry weight of the plant) has been so related. There appears to be no fundamental reason why such a relationship should not exist and the results presented in this paper suggest that growth as well as development of the early summer cauliflower plant can be related to accumulated temperature.

The base temperature selected for the accumulated day-degrees scale was the one that resulted in the smallest error variance when accumulated day-degrees above it were plotted against growth. It is considered that the base temperature determined in this way was probably also the lowest temperature at which growth or development could take place (i.e. 42° F. for growth and 32° F. for leaf initiation). This supposition cannot be fully tested without the use of controlled environment facilities but some support is given to it by the fact that leaf initiation was in fact observed to occur during periods in the winter when the temperature did not rise appreciably above 32° F.

The increase in dry weight of the whole plant from germination until curd maturity has been shown to be an exponential function of accumulated temperature. Thus, in the cauliflower plant the change from the vegetative to the generative phase of growth did not influence the relative growth rate of the plant, although work on other crops has shown that the growth curves may be characterized by a series of exponential segments which were related to physiological growth stages of the plant (Hammond and Kirkham, 1949; Hansen and McGregor, 1954; and Klages, 1933).

The reduction in leaf weight caused by the senescence and death of the older leaves, when there were no new leaves to take their place, resulted in a reduction of the overall growth rate of the whole plant. Although the fact that curd maturity coincided with the time of maximum leaf area of the plant suggested a possible causal relationship, the present data were insufficient to establish this relationship more closely.

In a previous paper the size of the curd at maturity was shown to be related to the soil moisture regime under which the plant had been grown and to the leaf area of the plant at maturity (Salter, 1959). In the present work an examination was made of the relationship between curd growth and leaf growth, and between curd growth and

that of the remainder of the plant. The relationships are shown in Figs. 7 and 8. When the weights of the organs are plotted against each other on logarithmic co-ordinates the curves appear to be linear and this suggests that growth was allometric (Reeve and Huxley, 1946), the slope of the line representing the relative growth rates of the organs. The relationship between curd and leaf growth was linear from the time of curd initiation until curd maturity, i.e., while both organs were growing.

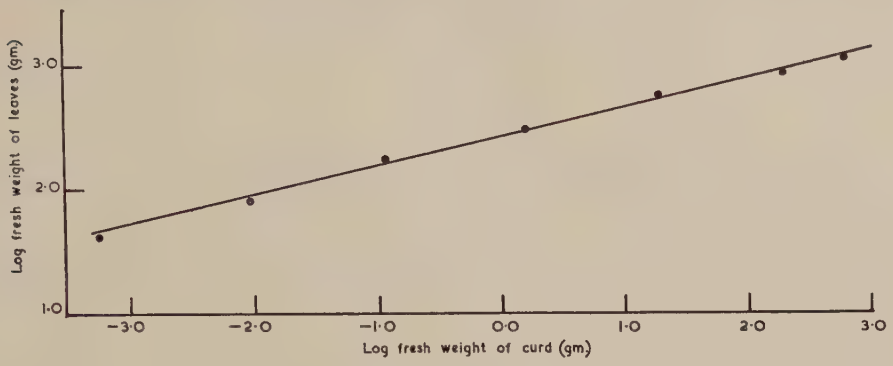

FIG. 7.

Allometric relationship between vegetative growth and curd growth for 1957/58 plants. Means of 40 plants.

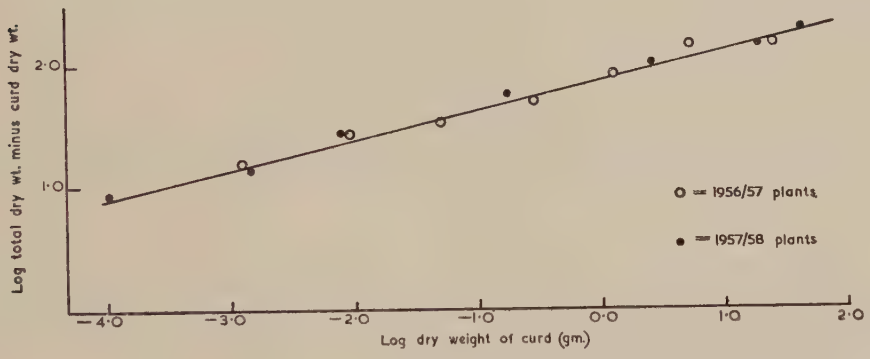

FIG. 8.

Allometric relationship between vegetative growth and curd growth. Means of 10 plants.

After this stage the leaves began to senesce and the relationship was no longer allometric.

In the cauliflower plant, growth is determinate in form, for after curd initiation has taken place no more leaves are formed and increase in leaf area results solely from leaf expansion. As the maximum leaf weight coincided with the stage of curd maturity and as growth of the curd was allometrically related to that of the leaves, it can be concluded that the size of the curd at maturity will be closely related to the

total amount of leaf material present; evidence to support this has been presented in a previous paper (Salter, 1959).

The present work has shown that the growth of the cauliflower plant and its principal organs can be expressed as functions of a simple meteorological parameter, viz. accumulated temperature, when edaphic factors are not limiting growth. This has enabled comparisons of plant growth to be made from year to year and has shown that temperature influenced the growth of the early summer cauliflower more than any other climatic factor when soil moisture was not limiting growth.

SUMMARY.

Analyses were made of the growth and development of whole plants and curds of early summer cauliflower grown under variable climatic conditions in the field. Accumulated measurements of the different climatic factors making up the weather were used to provide "time" scales against which to plot the growth of the plants. This enabled comparisons to be made of plant growth from year to year and provided information on the relative importance of certain of the variables in influencing growth and development.

Growth of the early summer cauliflower plant, from germination in October until the curd was mature in June, was shown to be exponentially related to accumulated day-degrees above a base temperature of 42° F., the growth curve until flowering time being logistic in form. The growth of the curd was also closely related to accumulated temperature in both years and the relationship between curd growth and leaf growth was allometric until the curd was mature. The time of curd maturity was coincident with that of maximum leaf weight, progressive senescence of the leaves occurring thereafter.

ACKNOWLEDGMENTS.

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SEASONAL CHANGES IN THE UPTAKE AND DISTRIBUTION OF MINERAL ELEMENTS IN APPLE TREES

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A DETAILED knowledge of the course of absorption of nutrient elements by fruit trees is of value to the grower in managing his orchard, and to the research worker in seeking to interpret the results of nutrition experiments in the field. The uptake of these nutrient elements from sand or water culture may be followed by observing the changes in chemical composition of the nutrient solution, but the investigator can never be sure that such artificial growing conditions do not themselves affect the mode of growth of the tree and consequently the course of nutrient absorption.

It was therefore decided that field-grown trees should be used, which immediately raised problems of sampling. It was proposed that whole trees should be harvested at monthly intervals throughout the year and separated into various parts for chemical analysis, so that the total uptake and the distribution within the tree of a range of elements could be followed throughout one annual cycle.

A small plantation of five-year-old apple trees was due to be grubbed and this provided the opportunity to make such a study; unfortunately they were not of commercial varieties, but were trees originally planted for another experiment and consisted of an apple rootstock variety worked as scion on two actual rootstocks.

It is impossible to state definitely that data obtained from such trees are likely to be characteristic of normal orchard varieties but, as the apple rootstocks M.IX and XVI must be regarded as varieties rather than separate species, it seems unlikely that the differences between the scion used in this experiment and the more usual varieties would be greater in degree or kind than between two commercial varieties, say Cox's Orange Pippin and Worcester Pearmain. So that, until more knowledge is available, it would seem reasonable to suppose that the results obtained with these worked trees are indicative of what happens in orchard trees of about the same age. It is quite likely that, as trees grow older and carry heavier crops in relation to vegetative growth, the uptake and movement of elements in the tree would be modified. Harley *et al.* (4) suggest, for example, that shoot growth and crop yield depend as much on reserve materials stored in the tissues of the tree from previous years as on current uptake of nutrients and, as the trees grow older, the importance of reserves would presumably increase.

The main experiment was done on the combination M.IX/XVI with a subsidiary one on M.IX/IX; thus the scion in both cases was M.IX. The two rootstocks exercised their characteristic influences on growth of the tree, that on M.XVI being much the more vigorous in habit (Fig. 1). The two rootstocks were expected to give results for absorption of nutrients which were quantitatively different but whether they would differ qualitatively was for determination.

PLATE I.

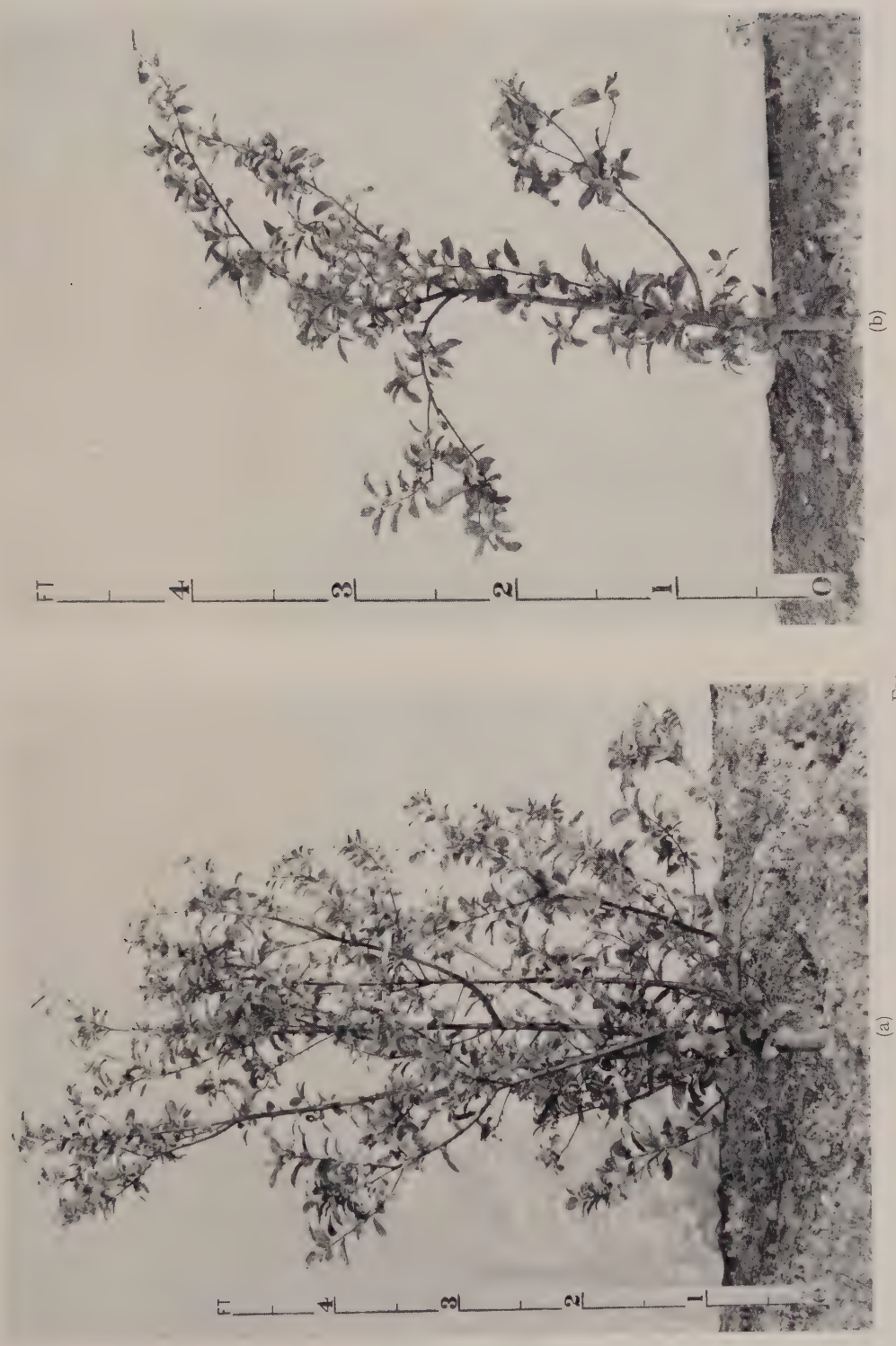

Fig. 1.
Typical specimens of trees of (*a*) M.IX/XVI and (*b*) M.IX/IX in September.

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Experimental procedure.

Apple rootstocks M.IX and M.XVI which had been reciprocally worked in all four combinations M.IX/IX, M.IX/XVI, M.XVI/IX and M.XVI/XVI were planted as one-year-olds 3 ft. apart in two rows on 2nd December 1952. For the purpose of the present experiment it was decided that only the two combinations M.IX/XVI and M.IX/IX should be used from the plots shown diagrammatically in Fig. 2. There

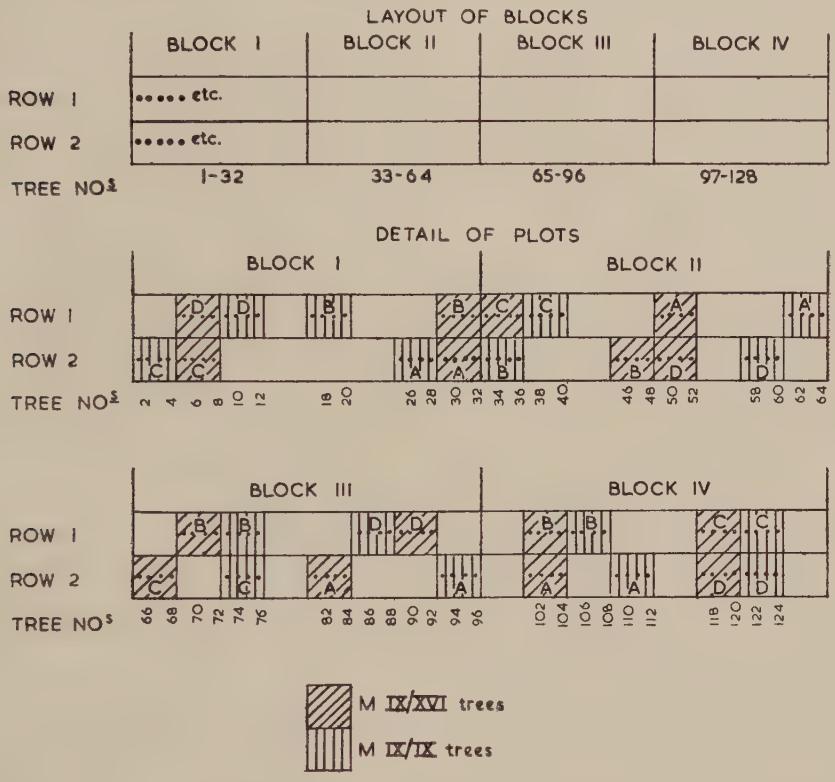

Fig. 2.

Experimental layout showing plots A to D arranged in randomized blocks. The blank plots contained trees not used in this experiment.

were four blocks each containing four plots A, B, C and D of each combination. Each plot contained four trees, one of which was sampled at a time. On each sampling occasion one tree of M.IX/XVI was taken from each block, from Plot A in the first month, from Plot B in the second month etc., and from Plot A again in the fifth month and so on. The M.IX/IX trees were sampled in the same way. The sampling occasions were arranged to be on or near the last day of each month with an extra occasion on 11th to 12th June because past experience had indicated that rapid changes occur about mid-June.

The size and form of the two types of tree sampled may be judged from the photographs of average specimens in Fig. 1. During their four to five years in the

plantation the trees were unpruned and were supplied with 4 cwt./acre per annum of a mixed fertilizer consisting of sulphate of ammonia and muriate of potash. The soil was cultivated by hand digging in winter and hoeing in the summer. Sprays were used to control scab, aphid and red spider but attacks of mildew were rather severe in some years. In 1957, the year of sampling, the M.IX/IX trees blossomed profusely and were allowed to set fruit though the crop was very light. The small amount of blossom on the M.IX/XVI trees was picked off on 5th April at the pink bud stage and late blossoms on 17th April.

The trees were lifted with care to avoid undue disturbance of those on either side while digging up as much of the large roots as possible; thus a considerable portion of root was left in the soil at each harvest, and no attempt was made to collect the fine roots. This was an unfortunate but unavoidable weakness in the sampling procedure.

After removing a tree from the site and before proceeding with sampling it was thoroughly washed to remove soil. Then the rootstock was sawn from the trunk at the union and its roots removed. Next, the leaves were stripped off and, after cutting off the current year's extension growth which was kept separate from the previous year's extension growth, the branches were finally separated from the trunk. As the growth of the trees had not been regulated, the division into branches and trunk was somewhat arbitrary because of differences in girth and occasional branching of the trunk near the union, but so far as possible a uniform standard was preserved. Sampling of the M.IX/IX trees was rather less detailed, and the current and previous year's extension growth were lumped together as were the trunk and branches. With the exception of the leaves every sample was washed in tap water, then in distilled water, and surface-dried for a brief period before determining its fresh weight. After weighing the total quantity of leaves, a sub-sample was cleaned and prepared for analysis by the method described by Mason (6). Sub-samples of the wood and roots were obtained by cutting the material into lengths of approximately 4 in. and taking discs from each length. Bark* was separated from wood which was cut into small pieces.

The fresh weights of all sub-samples were taken before placing in an oven for 24 hours at 80° C. The dried samples were weighed and by calculation the total dry weight of each original sample found. After grinding, the samples were analysed for total nitrogen, phosphorus, potassium, calcium and magnesium by reliable small scale chemical methods and the results expressed as percentages of dry matter. Total amounts of the elements in each plant part were calculated from the product of dry weight and percentage composition.

Results.

Figs. 3 to 9 show the variation in concentration of each of the elements N, P, K, Ca and Mg, throughout the year, in the various parts and in the whole tree. Each point plotted is the mean of values for four trees (one from each block). Results for potassium and calcium on M.IX/IX are given, as they differ in certain respects from those of the other tree combination ; for the other three elements results for the M.IX/XVI trees only are given as the behaviour of the two types of tree was generally similar.

* This term is used to include all tissue outside the cambium.

The presentation of results for the actual total amounts of each element is complicated by the fact that there was considerable variation in the size of the 52 M.IX/XVI trees and an even greater variation in size of the 52 M.IX/IX trees. The effect of such variation may be eliminated by expressing results for the whole tree as percentages of dry matter (see foot of Figs. 3-9) but when this is done it gives no real idea of the actual amounts of elements absorbed or lost by the tree. It is very desirable to obtain information on the time of year and rate at which the major nutrient elements move into and out of the tree as a whole; such information must be expressed in terms of actual amounts of each element and, in order to achieve a reasonable degree of accuracy, either the trees must be very uniform in size and behaviour or a very large number of them must be sampled and analysed. Since neither of these requirements was fully met in the present experiment, it became necessary to apply a correction factor to allow for variation in tree size, and for this purpose the weight of dry matter in the wood of the whole tree has been taken as the best available index of tree size. The correction was applied as follows : a mean figure for dry weight of the wood, excluding bark, for all the trees sampled from January to May inclusive and another mean figure for trees sampled from August to December inclusive were calculated. Information from other experiments (Maggs, private communication) indicated that the main increase in dry matter in wood occurs between the end of May and the end of August so, as a simple approximation, it was assumed that the dry weight increase was roughly linear between these dates and that before and afterwards no appreciable increase or decrease in dry matter occurred. On these assumptions it was possible to construct a curve showing the dry weight of an average tree at each sampling occasion. Then by simple proportion the actual amount of element present in the above-ground portion of the sampled trees was corrected to the amount which would have been present if all the trees had been of uniform average size. The corrected results are presented in Figs. 10 and 11.

If the mean values for total amount of element in the tree each month are plotted without applying a correction for tree size, the graphs which emerge for the two types of tree are different and the amounts of elements absorbed appear devoid of systematic progression. On the other hand, the graphs presented in Figs. 10 and 11, after correcting the amounts of elements for tree size, show remarkable agreement for the two tree types, especially for nitrogen and potassium. It will be noted that for every element there is a sharp maximum value at the end of July and attention should be drawn to the possibility that this might arise from or be accentuated by the method of correcting. It happened that all the trees of both types sampled in July were usually small ($\frac{1}{2}$ to $\frac{2}{3}$ of the weight of the general run), so the correction applied was large and consequently might have been excessive.

It would be unsound to make similar calculations for the various parts of the tree, since no reasonably satisfactory index of rate of dry matter increase could be adopted for an individual part of the tree ; thus movements of elements into and out of specific tissues can only be deduced from a consideration of the concentrations shown in Figs. 3-9. Nevertheless these do give a fair indication of such movements, especially between plant parts which are growing at about the same rate; but, of course, there must always be some doubt about whether a fall in concentration should be interpreted as a loss of the element to another part of the tree or as an effect due entirely to dilution of a fixed amount of the element.

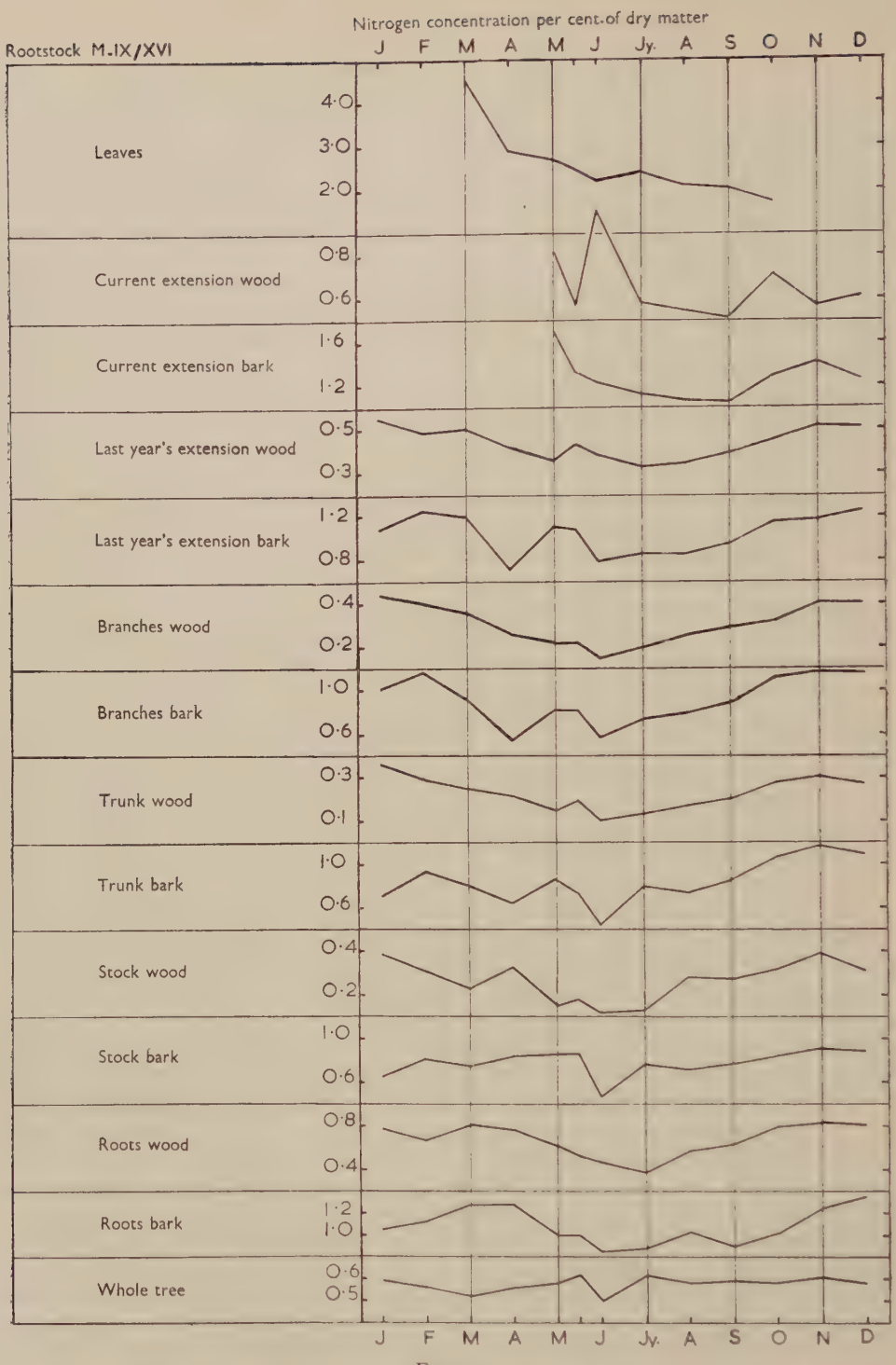

FIG. 3.

Nitrogen. Concentration of the element in various parts and in the whole of the tree at monthly intervals throughout the year. Points indicate the *end* of each month and in June extra samples were taken about mid-month. The term "bark" is used to indicate the whole of the tissues outside the cambium and "wood" means the xylem and heart wood.

Nitrogen (Fig. 3).

The concentration of nitrogen, per unit of dry matter in the whole tree, varied very little over the year, though there was a sharp fall in June to a minimum value. Maximum values occurred in the middle of June and at the end of July. The mean value was about 0·57% for the M.IX/XVI trees and about 0·74% for the M.IX/IX. With regard to the movement of the element in the plant there are two periods of special interest: about the end of April, when rapid leaf growth began, and again at the end of June, when shoot extension was vigorous. The sharp fall in nitrogen concentration in the whole tree to a minimum value at the end of June is clearly shown in Fig. 3 and it corresponds to a maximum in the wood of the extension shoots. There are simultaneous minima for nitrogen in the wood and bark of the older parts of the tree. This may be interpreted as a temporary withdrawal, from the older tissues, of nitrogenous compounds which are transferred to the extension growth.

A sharp fall in nitrogen concentration occurred in April in the bark of extension growth, branches and trunk (in this order of intensity). It seems that the nitrogenous compounds needed by young leaves may be supplied from the bark rather than the wood, the severest stress occurring at the point nearest to leaf formation. These withdrawals produced only a temporary deficit which was made good during the ensuing month.

The concentration of nitrogen in the leaves decreased fairly smoothly from the time of their appearance in March to leaf fall, while that in the bark of new growth fell to a minimum in August and then gradually rose to a value (about 1·2%) found in the bark of the older parts of the tree. The nitrogen concentration in the bark and wood of the older parts of the tree was built up to a maximum in the autumn.

The cycle for the total quantity of nitrogen in the whole tree is shown in Fig. 10. Absorption apparently commenced during April and reached a maximum in July. At the end of June there was a short period during which nitrogen seemed to be excreted by the tree, a suggestion which is discussed more fully below. During the month of July there was rapid reabsorption of the element and thereafter a gradual loss during the autumn mainly due to shedding of leaves, and in the winter and early spring months presumably by excretion through the roots.

Phosphorus (Fig. 4).

There is little which calls for special comment on the distribution of this element. The concentration in the whole tree varied slightly during the season about mean values of 0·07% for the M.IX/XVI trees and 0·095% for the M.IX/IX. Concentrations in the leaves and in the blossoms were high at the beginning of the season and fell fairly rapidly to a stable figure of about 0·2%. In the bark there was a sharp fall to a minimum concentration at the end of April coinciding with a similar fall in concentration of nitrogen ; this is apparent in the scion of each combination but not in the bark of the M.XVI stock. In the latter and in the woody parts of the trees the phosphorus concentration generally rose to a maximum in April followed by a minimum in May. The graphs for M.IX/IX trees (not reproduced) show this especially. It seems that phosphorus was being supplied in good concentration through the roots and wood but was being withdrawn from the bark of the shoots and young branches to support early leaf development.

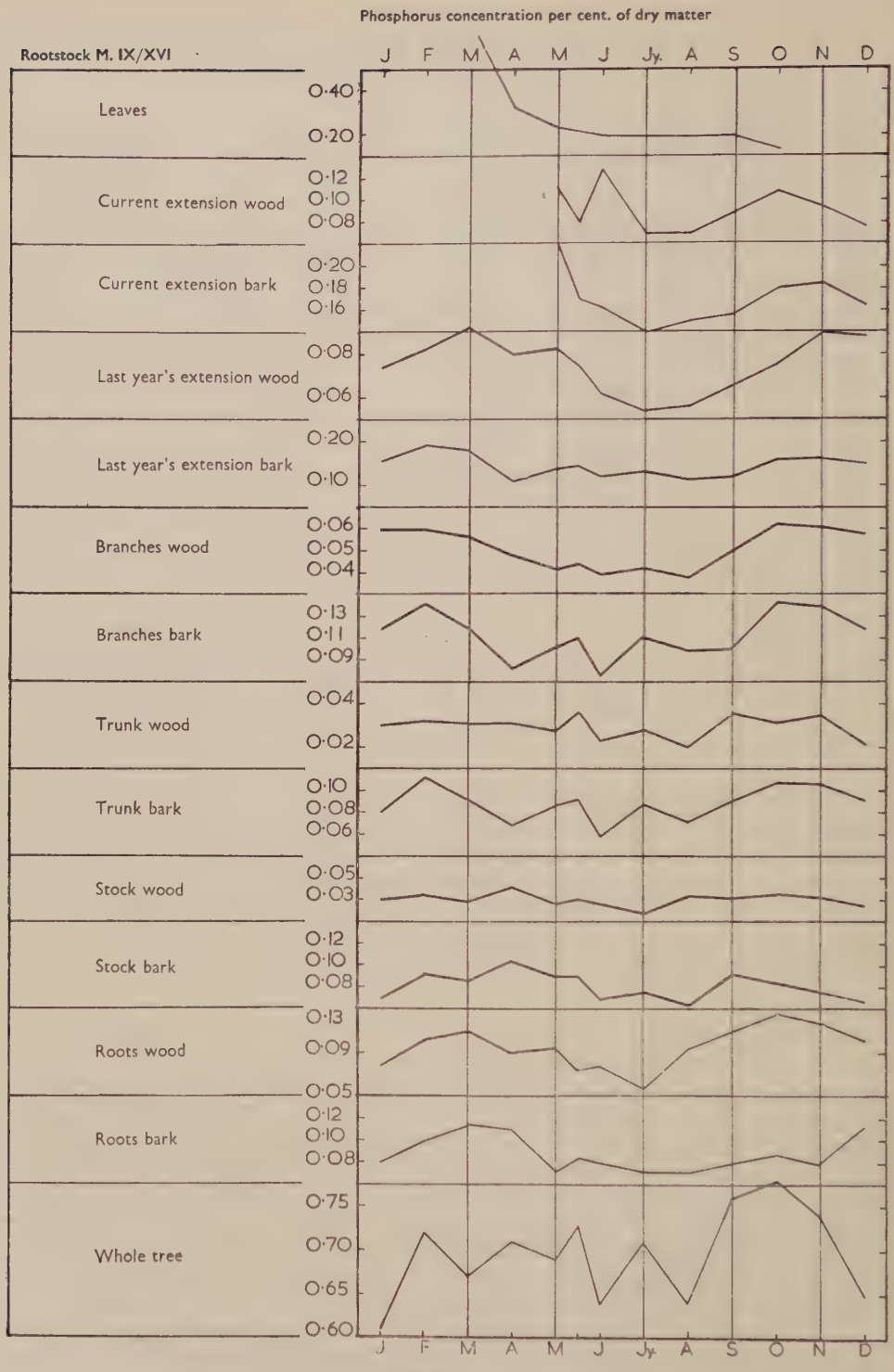

FIG. 4.

Phosphorus. See legend under Fig. 3.

Potassium (Figs. 5 and 6).

Unlike nitrogen the concentration of potassium, per unit of dry matter in the whole tree, varied considerably over the year, rising from the end of March to the end of July and falling again to a low value in the late autumn.

The distribution of the element in the two types of tree was dissimilar in certain respects, particularly with regard to concentrations of potassium in the whole tree and in the trunk and branches ; for instance the M.IX/XVI trees showed a peak at the end of May which did not occur with the other combination ; also in September potassium fell to a minimum value in the M.IX/IX trees but not in the others. On the other hand the graphs for wood and bark of previous year's extension growth are similar in shape. In April, coinciding with rapid leaf growth, there was a sharp fall in concentration of the element in the bark of shoot, branch and trunk. In Fig. 6 this is obscured because the older wood and bark were not separated but it is very obvious in the bark of the shoot. Concurrently there was a sharp rise in the bark and wood of the root. At the time of rapid shoot extension in the latter part of June there was a fall in concentration in the bark particularly of the older parts of the tree and, significantly, in the leaves. At the same time there was a rise to a sharp maximum in the wood of both the previous year's and current shoots. The graph of potassium concentration in the leaves follows roughly the same course for the two types of tree, falling to a low value at the end of June, then rising during the summer months, and falling again sharply before the leaves were shed.

The concentration of potassium in blossom and fruit fell regularly up to the end of July, after which the sampled trees carried no fruit. In that part of Fig. 10 relating to total potassium, after correcting for tree size, absorption of this element is seen to have proceeded continuously in both tree combinations from the end of March to the end of July, after which there was a continuous loss to the end of November. The amount of potassium remained practically constant during the winter months and early spring.

Calcium (Figs. 7 and 8).

The concentration of calcium in the whole tree of the M.IX/XVI combination increased continuously from March to mid-June and, after a sharp dip at the end of June, recovered and then fell gradually to the end of the year. This differs from the M.IX/IX trees (Fig. 8) for which there was a peak of calcium content in April followed by a trough in May ; also the fall from the July maximum was much more sharp. These differences are accounted for almost entirely by analogous concentration differences in the *bark* of the trunk, branches and roots which together contained the bulk of the calcium in the tree. The wood in all parts of both types of tree shows a peak in April (time of rapid leaf development) followed by a trough in May. At the end of June, and coinciding with vigorous extension growth, there is another but less pronounced peak in concentration in the wood and a corresponding deep trough in the graph for calcium in the bark. The graphs for the previous year's extension growth, showing wood and bark separately, are very similar for both types of tree; on the other hand the graphs for concentration of calcium in the whole tree are different, the deep trough appearing in May for the M.IX/IX and in June for the M.IX/XVI trees. It is shown below (Fig. 13) that the bulk of the calcium in the M.IX/XVI trees was in the bark and it is therefore natural that the low values in the

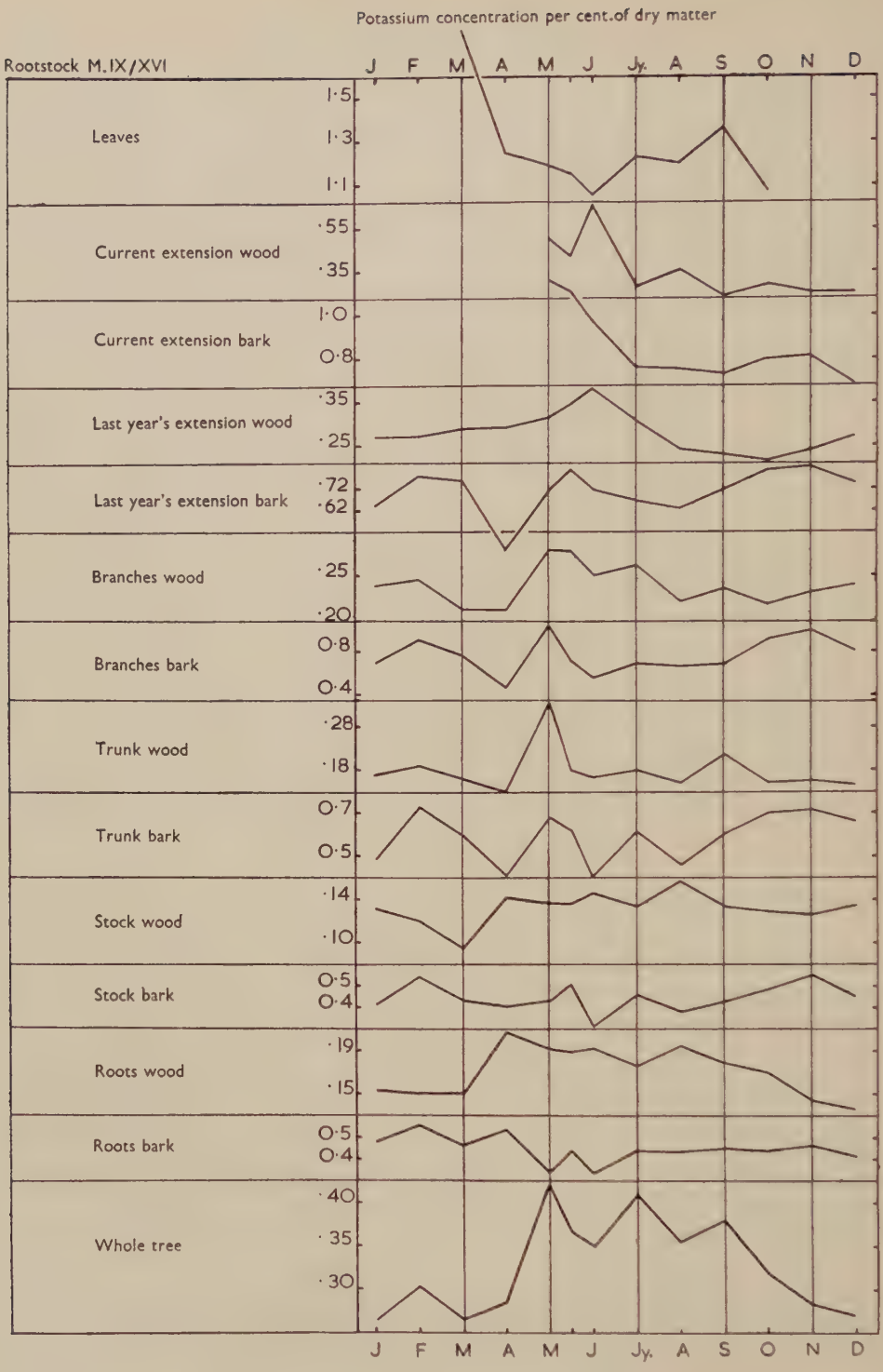

FIG. 5.

Potassium. See legend under Fig. 3.

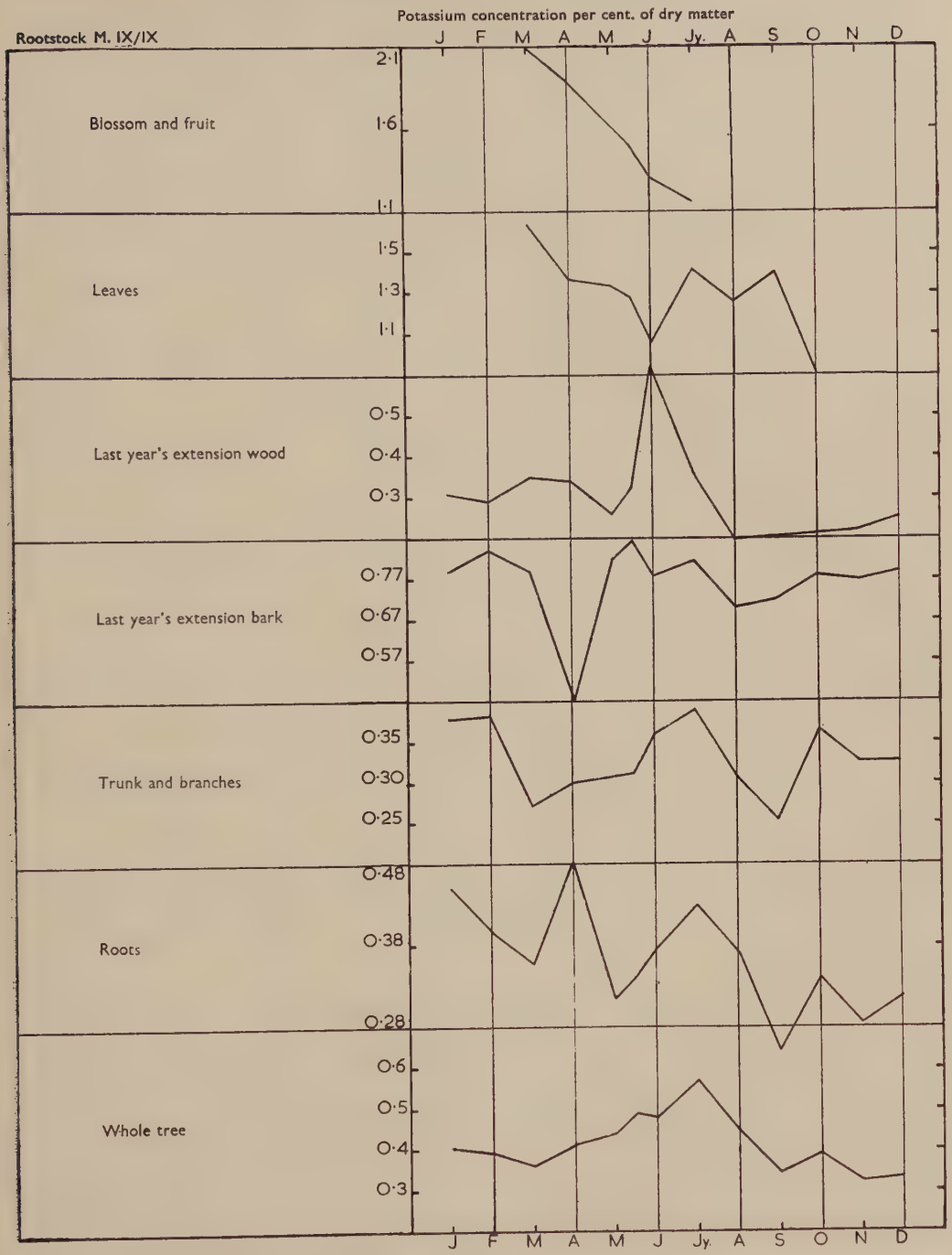

Fig. 6.

Potassium. See legend under Fig. 3.

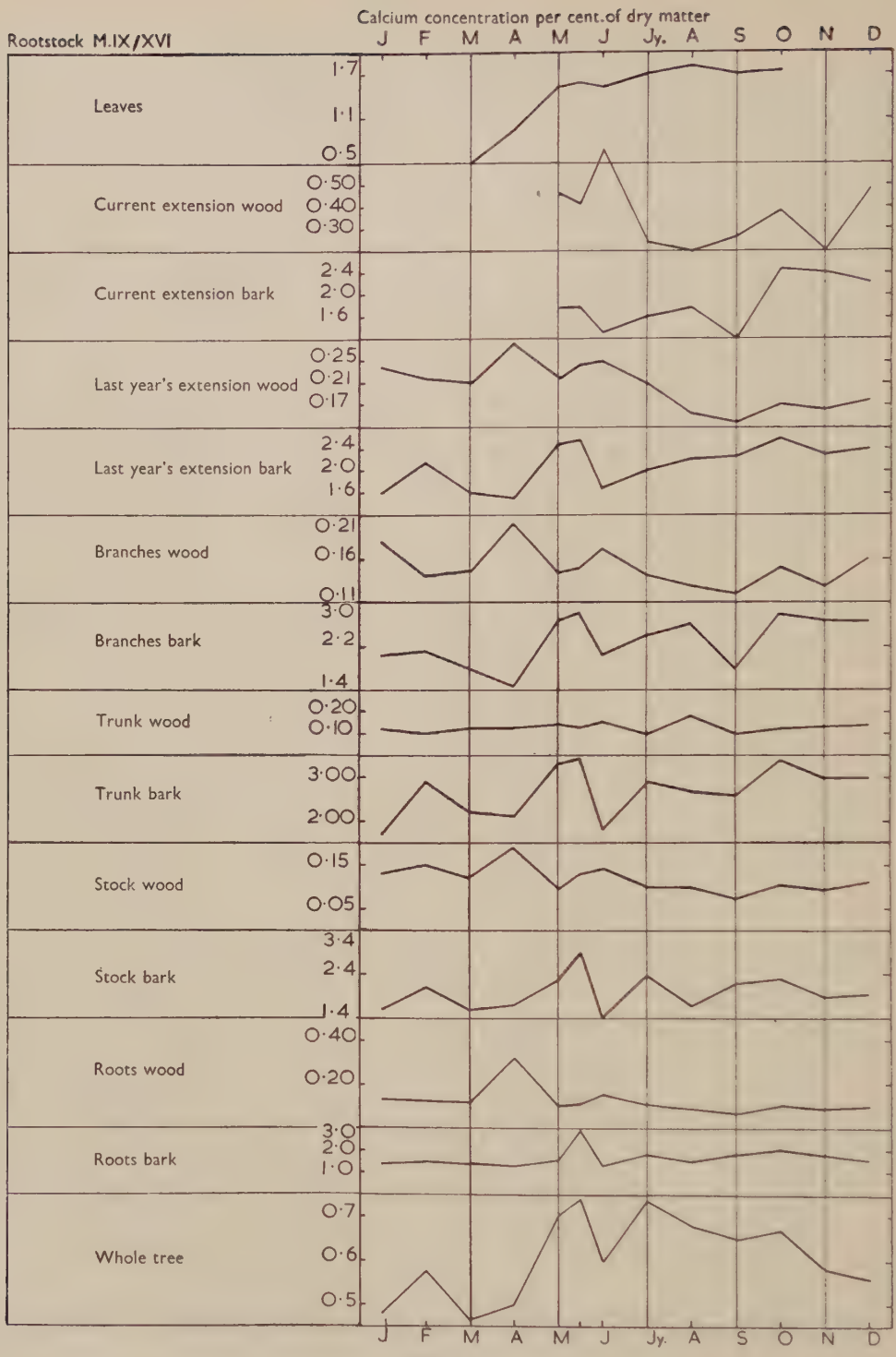

FIG. 7.

Calcium. See legend under Fig. 3.

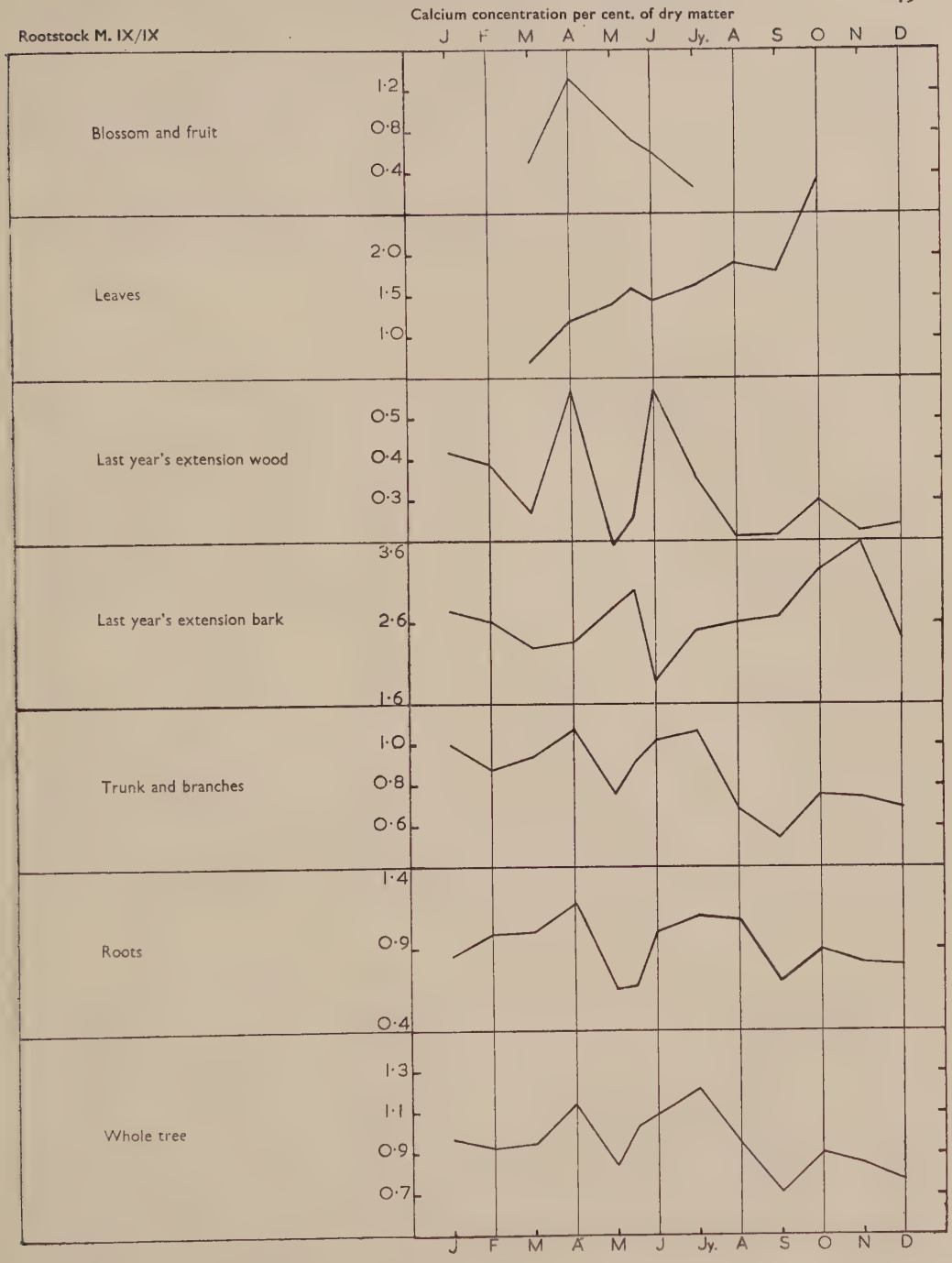

Fig. 8.

Calcium. See legend under Fig. 3.

bark produced a simultaneous low value in the whole tree, whereas low values in the wood barely affected the value for the whole tree. Since the deep trough in the graph for the M.IX/IX whole tree occurs in May and corresponds to the deep trough in the graph for *wood*, not bark, it suggests that the proportion of calcium in the bark of M.IX/IX trees was much smaller than in the M.IX/XVI trees. Unfortunately the trunk, branches and roots of the M.IX/IX trees were not separated into wood and bark, and the present body of data is insufficient to resolve the point. The M.IX/IX trees blossomed profusely and produced relatively little shoot growth compared with the M.IX/XVI trees ; it is possible that the differences in calcium concentration are associated with that fact.

Magnesium (Fig. 9).

It is again evident that the two periods when well-marked changes occurred are the end of April and the end of June. In the woody parts of the tree, concentrations were higher in the winter and early spring than in the summer. Since the bulk of magnesium in the tree was contained in the leaves, it was to be expected that the graphs for concentration and actual amount of element in the whole tree (Figs. 9 and 10) would show a rise from April to a maximum in July and then a decline as the leaves were shed.

During the month of May leaf growth was rapid and the heavy demands for magnesium at this time were met by withdrawals of the element from the wood of the stock and root.

Blossoms and fruit.

The M.IX/XVI trees were deblossomed, but from the profuse blossom left on the M.IX/IX trees very little fruit was set. The concentration of potassium in the blossom was 2·11%, falling gradually as the fruitlets developed to maturity (Fig. 6). The sequence for calcium was different, as the concentration in the fruitlets was much higher than in the blossom and it fell by dilution due to growth (Fig. 8). Nitrogen and phosphorus concentrations followed the same course as potassium while magnesium resembled calcium in its behaviour.

DISCUSSION.

Mochizuki and Hanada (7), working with young apple trees from April to November, conclude that at the beginning of leaf development the supplies of nitrogen, phosphorus and potassium used in the formation of new tissue are derived mainly from tree reserves, principally the bark of branches and stem. Our results support this conclusion and also the suggestion of these workers that the growth of young apple trees occurs in three distinct phases. We would, however modify their description as follows : (1), a period of formation of new tissue, the materials for which are drawn from reserves in the tree laid down during the previous year or years ; (2), a period, toward the end of May, when the new leaves are able to contribute photo-synthesized compounds from raw materials being currently absorbed through

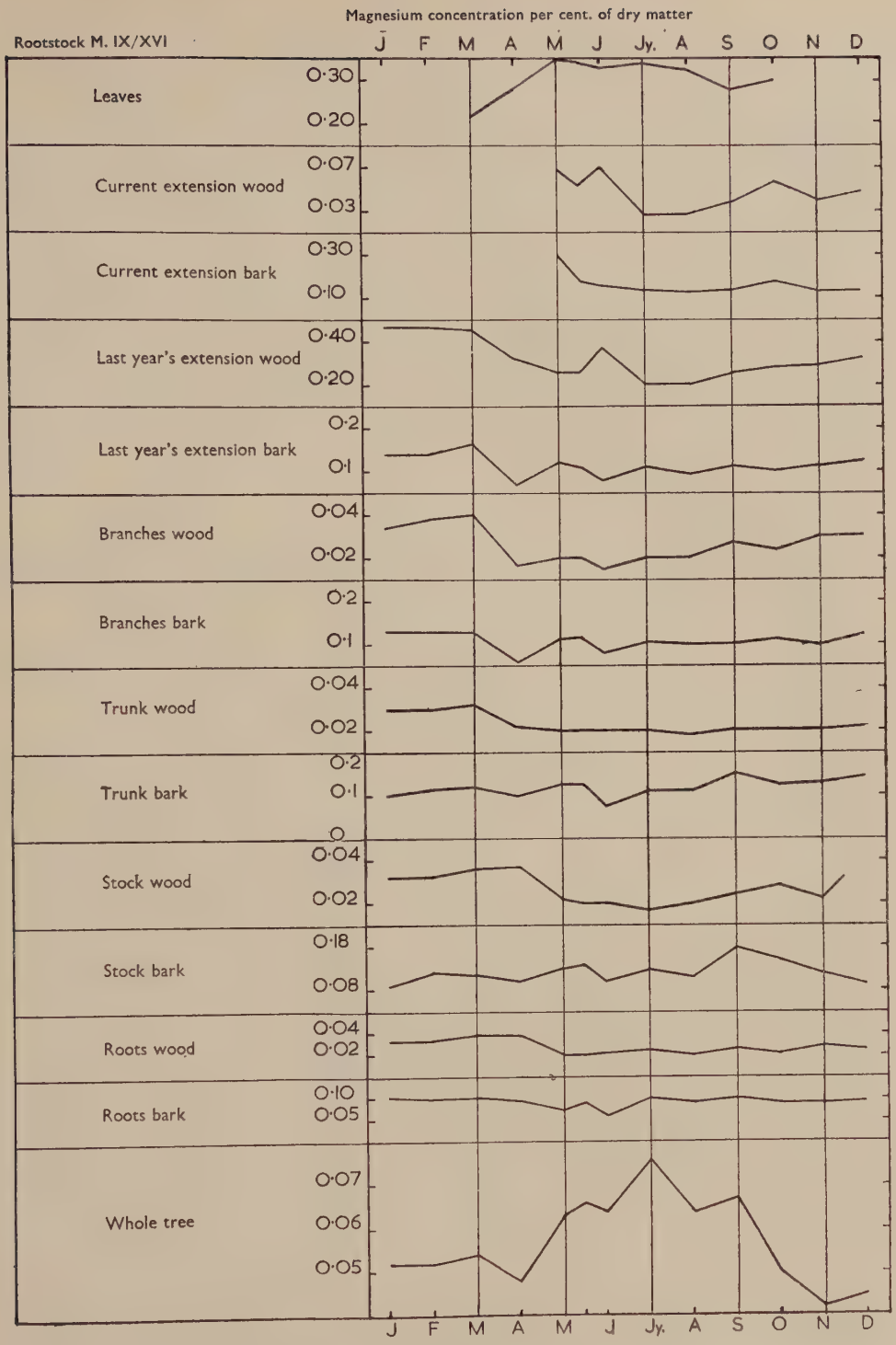

FIG. 9.

Magnesium. See legend under Fig. 3.

the roots and leaf surfaces. These newly-formed compounds are translocated to support the formation and expansion of further new tissue up to about the end of August ; (3), with the cessation of further growth, compounds of the nutrient elements are redistributed in the tissues, in some of which the concentrations are increased, e.g., nitrogen in the branches, magnesium in the younger wood, and calcium in the bark.

This hypothetical sequence is derived from our data on the deciduous apple tree. On the other hand Cameron *et al.* (2), working with citrus trees which bear new leaves in flushes at irregular intervals through the year, found an almost random variation in concentration of elements with time. They estimated that from a third to a half of the total of nutrient elements was in the leaves and, since leaves were continually ageing and being replaced by new ones, this apparent random variation is hardly surprising.

Mobility of elements.

We have suggested from our results that tissues where a sharp fall in concentration occurs over a short period, such as a month, are functioning as storage organs

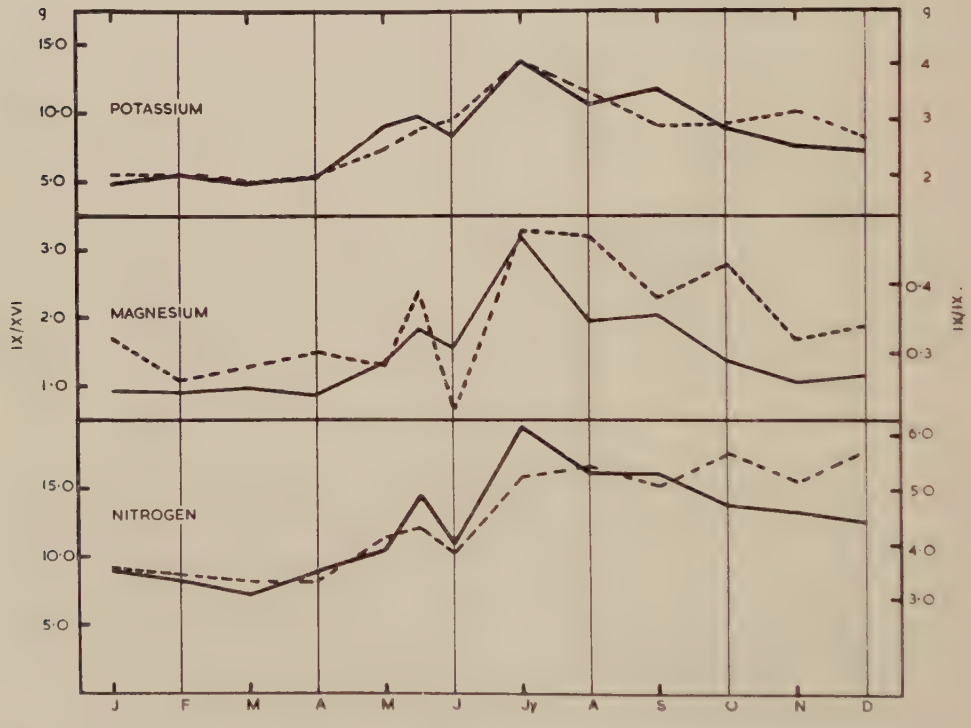

FIG. 10.

Amounts of nitrogen, magnesium and potassium, after correcting for tree size, in the above-ground portion of trees sampled throughout the year. Continuous line M.IX/XVI. Dotted line M.IX/IX.

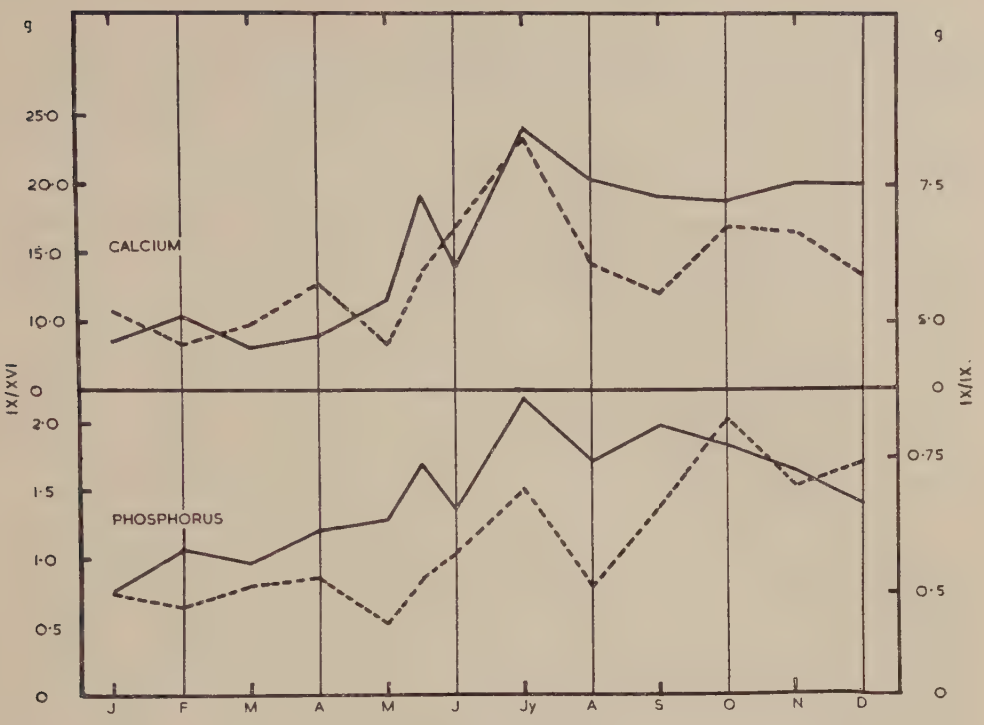

Fig. 11.

Amounts of calcium and phosphorus, after correcting for tree size, in the above-ground portion of trees sampled throughout the year. Continuous line M.IX/XVI. Dotted line M.IX/IX.

whose contents are temporarily depleted. If the fall in concentration were due to dilution by growth, it would require a large amount of growth over a short period ; dilution of a fixed amount of element by growth would probably be recognized by a gradual decline in concentration over several months.

It would be generally agreed that the mass movement from one group of tissues into another at certain critical times is possible for the elements nitrogen, phosphorus, potassium and magnesium at least, but, in view of current ideas about the immobility of calcium, it may be doubted whether the latter element is likely to move in quantity. From the data for actual amounts of calcium in the bark of trees sampled on 11th and 25th June (Table I) it is evident that, in the space of a fortnight, the actual amount of calcium in the bark of most parts of the tree was substantially reduced, indeed by as much as 41% in the trunk, while the actual weight of bark increased. It has not been possible, on account of the variation in tree size, to draw up a balance sheet for movement of this element but evidently some of it was transported from the bark to the wood of the tree. Evidence from the M.IX/IX trees confirms this conclusion but is restricted to the bark of the previous year's growth, as other parts were not divided into wood and bark.

Thus it seems justifiable in this case, and probably in most others, to interpret a *sharp fall in concentration* of an element in particular tissues as a net withdrawal of that element from the tissues.

TABLE I.

Changes in the amount of calcium in the bark of apple trees between 11th and 25th June.

Total amount of:	Sampling date	M.IX/XVI trees			M.IX/IX trees
		Previous year's shoots	Branches	Trunk	Previous year's shoots
Calcium	11th June, 1958 (*a*)	5·55	22·03	12·03	2·77
	25th June, 1958 (*b*)	4·83	19·77	7·06	2·41
	Decrease in calcium content (*a-b*) ..	0·72	2·26	4·97	0·36
	Statistical significance (P) ..	N.S.	N.S.	5%	—
	Decrease as percentage of (*a*) ..	13·0	10·3	41·3	13·0
Dry matter	11th June (*c*)	231	784	353	85
	25th June (*d*)	310	1,015	387	129
	Increase in dry matter content (*d-c*)	79	231	34	44
	Increase as percentage of (*c*) ..	34·2	29·5	9·6	51·8

Bollard (1) studied the seasonal movement of elements in the tracheal sap of the branches of apple trees but did not include calcium in his analyses. Bearing in mind that the amount of each element in the tracheal sap is only a small proportion (say 2%) of the total amount present in the branches, one would not expect the seasonal changes in the tracheal sap and in the whole branches to be necessarily similar. Nevertheless, the two periods of special activity which we have distinguished in April and June can in fact be readily identified in Bollard's graphs (October and December respectively in the southern hemisphere), but here they occur as peaks and not as troughs, suggesting that at these two periods compounds of the various elements are converted into a soluble form and then conveyed in the sap stream to the actively growing parts of the tree. The fact that, in Fig. 7, there are troughs in the graph for branch bark in April and June coincident with peaks in the graph for branch wood, is consistent with this view.

Excretion of elements.

At the end of the season when growth ceases there appears to be a redistribution of nutrients within the tissues and at the same time an excretion of excess of elements, either by loss of leaves or by other means.

In agreement with Mochizuki and Hanada we found that in October the concentration of potassium fell to a low value in the wood of the previous year's growth and the older branches. Since there was also a sharp fall in leaf concentration, so that a considerable amount of potassium was returned to the tree, and since the concentration of potassium in the whole tree decreased, it would appear that excretion took place through the roots and could not be explained by growth dilution as suggested by these authors. With the M.IX/IX trees, both concentration and total amount of potassium decreased earlier, i.e. during August and September (Figs. 6 and 10).

Phosphorus accumulated in the permanent parts of the tree during the months of September and October in amounts which more than balanced any loss from the ageing leaves. During this period considerable absorption of this element occurred through the roots, only to be excreted again later.

The excretion of nutrient elements by the shedding of fruit and of leaves is a commonplace concept, but that any considerable excretion of elements through the roots of trees may occur is not generally accepted, though the possibility is referred to by Colby (3) when reviewing the work of Bauer and others on mineral salt absorption. The results which we have presented in this paper lead us tentatively to the view that absorption and excretion of nutrient elements occur continuously over most of the year and that sometimes one and sometimes the other predominates. This is illustrated by the loss of nitrogen by the whole of the above-ground portion of the tree between 11th and 25th June shown in Fig. 10. It is possible that the nitrogen moved only as far as the root system but this seems unlikely since analysis of the larger roots showed a fall in concentration of nitrogen over the period considered.

Mori and Yamazaki (8) studied the uptake of nitrogen, phosphorus and potassium by several varieties of young apple trees when grown in water culture and their results, covering the period April to December, may be compared with ours. It is interesting to find that they recorded a period, roughly coincident with ours, when nitrogen was apparently excreted by the variety Rall's Janett. While our results on the course of absorption of nitrogen and potassium are somewhat at variance with theirs we do agree over phosphorus. However, some disagreement may be expected in view of the differences in varieties and cultural techniques.

The results of investigations carried out by Karmarkar (5) on current season's extension growth of Newton Wonder apple trees sampled at monthly intervals and examined for total nitrogen content, may be compared with our results expressed in Fig. 3 (top portion). They will be found to agree remarkably closely. Also the results of Vaidya's (9) work on the P, K, Ca and Mg content of current extension shoots of Lane's Prince Albert, Worcester Pearmain and Bramley's Seedling varieties of apples worked on a range of rootstocks agree fairly well with the results for similar parts of the tree given in this paper.

The fact of such agreement lends support to the belief, expressed earlier, that the results from the studies reported here may be considered as typical of the course of mineral uptake of young apple trees grown in the field.

Distribution of elements in the tree.

The distribution of each of the five elements in various parts of the tree, as percentages of the total, is shown in Figs. 12 and 13 by histograms for two months of the year, the first in February before the annual growth cycle had commenced and the second at the end of August when the season's growth had practically ceased. In February (Fig. 12) the nitrogen and phosphorus were held mainly in the wood of the roots and branches while potassium, magnesium and calcium (especially the last) were held mainly in the bark of the branches. In August (Fig. 13) the proportion of each of the elements in the leaves is seen to be large (almost 50% for magnesium) in spite of the small proportion of total dry matter which they contributed.

SUMMARY.

(1) Six-year-old apple trees M.IX/XVI and M.IX/IX, grown three feet apart in rows, were lifted, one from each of four blocks, on each of twelve occasions at approximately monthly intervals throughout the year.

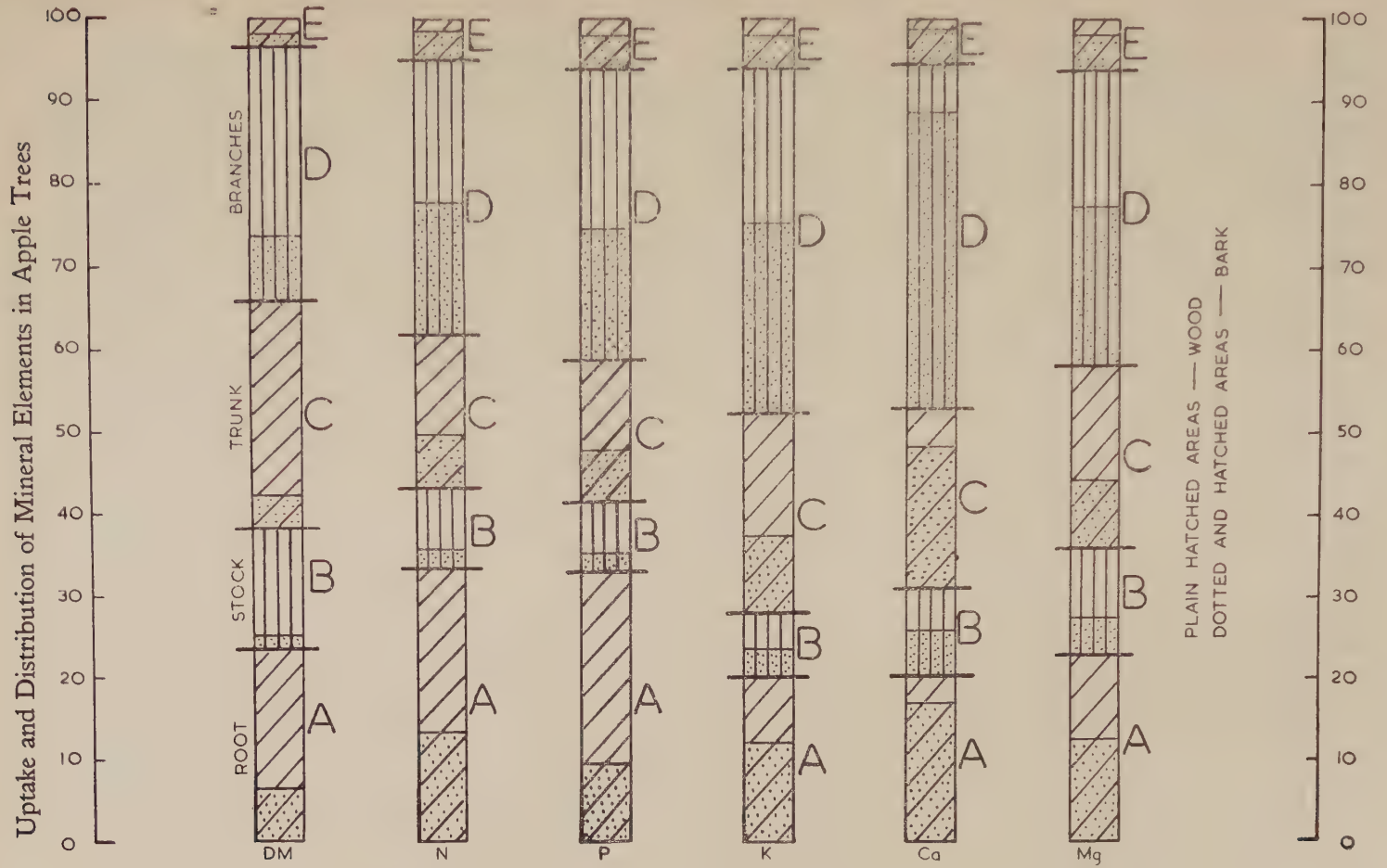

FIG. 12.

Distribution of dry matter, nitrogen, phosphorus, potassium, calcium and magnesium in various parts of the tree, expressed as percentages of the amounts present in the whole tree in February. See Figs. 3–9.

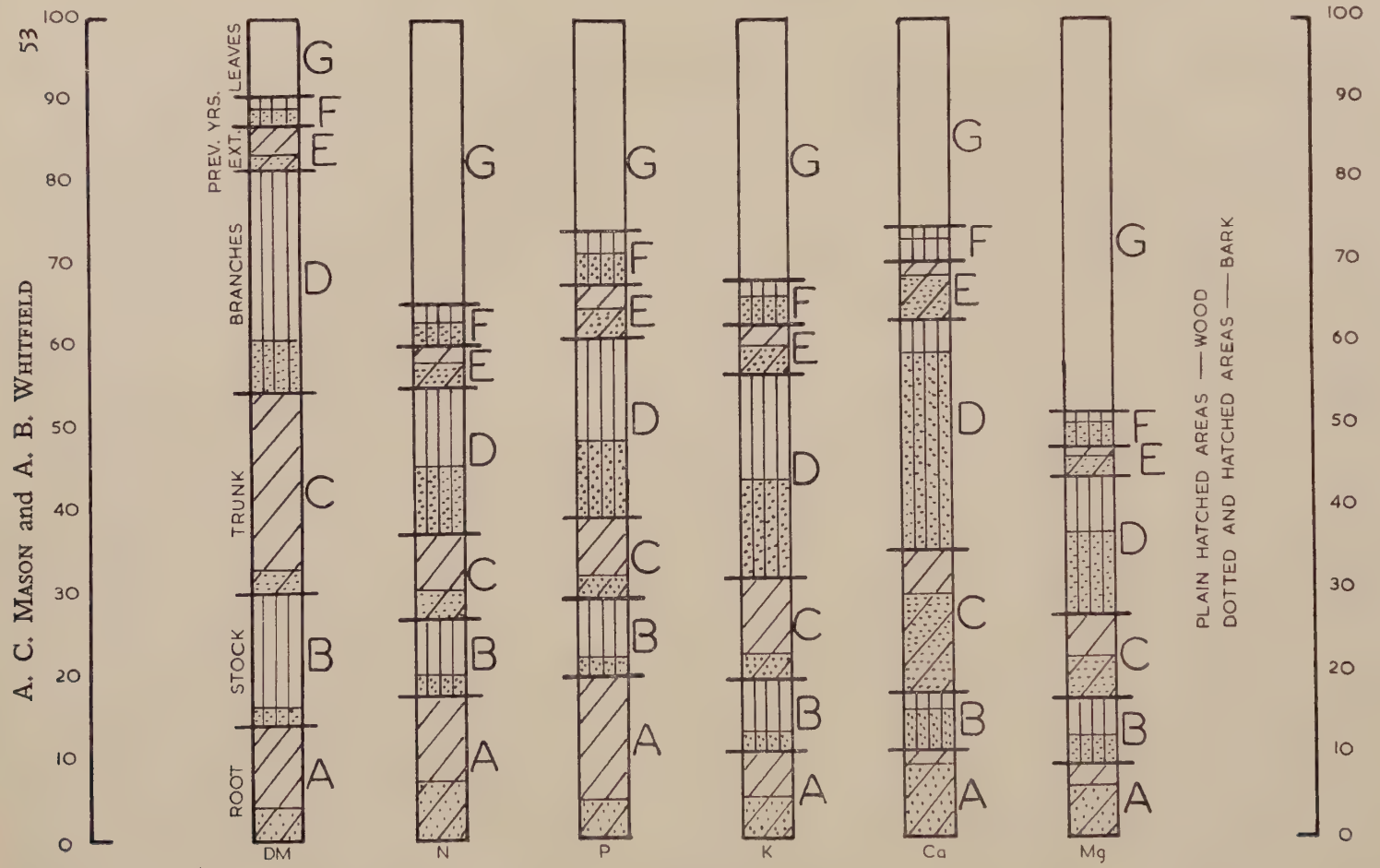

Fig. 13.

Distribution of dry matter, nitrogen, phosphorus, potassium, calcium and magnesium in various parts of the tree, expressed as percentages of the amounts present in the whole tree in August. See Figs. 3–9.

(2) Each tree was divided into several parts and samples analysed chemically for percentage of N, P, K, Ca and Mg. Records were kept of fresh weight and dry weight of the various parts and by calculation the actual amounts of the five elements in the whole tree were determined.

(3) Two periods of special activity may be distinguished, at the end of April and the end of June, when the concentrations of the five elements changed appreciably over a short time in most of the tissues. These two periods coincided with the onset of rapid leaf growth (April) and of shoot growth (June).

(4) The uptake of most elements commenced at the end of April or May and reached a maximum at the end of July or August, after which there was a loss of elements by the tree; uptake of nitrogen commenced about a month earlier. The question of excretion through the roots as well as by leaf shedding is briefly discussed. The fact that no net absorption of N, P, K, Ca or Mg was recorded in the autumn will be of practical interest to fruit growers, though it was noted that the concentration of nitrogen in wood and bark of the older parts of the tree increased during the autumn.

(5) At the end of the summer the bulk of each element in the tree was contained in the following organs : nitrogen in the leaves, branches and roots ; phosphorus in the leaves, branches and roots ; potassium in the leaves and branches ; calcium in the leaves and bark ; magnesium in the leaves.

ACKNOWLEDGMENTS.

We wish to acknowledge our indebtedness to the members of the Plant Analysis Section who assisted in the preparation and analysis of samples of plant material, to Mrs. B. M. Showler who summarized the large amount of data and to Misses M. E. Jenner and G. Clinch who prepared the diagrams.

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IMPROVING FRUIT TREE EXPERIMENTS BY A PRELIMINARY STUDY OF THE TREES

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With fruit trees it is not easy to conduct really accurate experiments because of the variability in the plant material. For single-tree plots the coefficient of variation in crop is often as high as 25%, so about forty replicates are needed to show a difference of 10% ($P = 0{\cdot}05$). So large an experiment is scarcely practicable, yet a sustained reduction in cropping of this order could be most important.

Various suggestions can be made to counter this difficulty. Thus one-tree plots are not essential and larger ones are less variable. This is true, but if maximum information is to be obtained from an area or a given number of trees the smallest plots possible must be used (Smith, 1938 ; Pearce, 1955). Basically the solution must lie in producing more uniform trees, but progress is slow. In the past there were sources of variation, e.g. that due to seedling material, of such magnitude that they could readily be detected despite all the others ; at some point, however, this must come to an end, all sources of variation being then small and each difficult of detection on account of the rest.

In this paper attention will be given to the method of " calibration ", i.e. the laying down of experiments on trees that have been under observation for a period so that their individual characteristics are known. Then the performance of trees under various treatments can be considered in relation to what might have been expected of them had no differential treatments been applied, the appropriate statistical technique being that of the analysis of covariance. This approach is not new, as a bibliography of the subject shows (Pearce, 1953) ; the name was suggested about ten years ago (Pearce and Taylor, 1950).

The assumptions that underlie this approach need some consideration. One is that the measurements to be used for calibration have not themselves been affected by the treatments. If they have been made before the treatments were applied, this will cause no questioning, but caution is needed with those made afterwards. Also serious is the possibility that the differences observed during the calibrating period shall not alter the effects of the treatments. Thus, if during calibration some trees are making little growth, in a subsequent pruning expriment those trees might be stimulated into action by some treatments and not by others, the treatments having much the same effect on trees initially growing normally. Consequently, when there are large initial differences between plots, the experimenter may decide to discard some of the original material as unsuitable. However, if only ordinary variation is encountered during calibration, it will usually be safe to use the analysis of covariance ; perhaps the most important subsidiary use of a calibrating period is the assurance it gives that no abnormal trees have been included.

Data used.

In this paper data will be used from three trials at East Malling of Lane's Prince Albert and Cox's Orange Pippin apple, and Conference pear. Some results with oranges (Parker, 1942) will also be used.

Lane's Prince Albert apple.

In this trial there were 24 similarly treated trees on M.XII, arranged in four blocks each of six trees. All figures relate to variation between trees within blocks. The trees were planted as one-year-olds in the winter of 1919-20 and the first appreciable crop, namely 4·9 lb. per tree, was obtained in 1927. Crops were very low in 1935 and patchy in 1941, both frost years ; they were poor in 1931 also. During the winter of 1946-47 the plantation was thinned, leaving only 14 of the original trees.

Cox's Orange Pippin apple.

To avoid attributing all differences between trials to differing species, a second apple trial was examined.

The data were taken from a rootstock trial of Cox's Orange Pippin planted as one-year-olds in February 1922. There were six blocks, each of eight trees on the same rootstock, two blocks on each of the rootstocks M.V, M.VI and M.X. In 1935 there was no crop on account of frost and other poor years were 1938, 1941 and 1944. Up to 1930 there was only about 15 lb. of fruit per tree, but thereafter, despite frost, cropping increased, especially immediately after the trees were thinned, reaching a maximum in 1947-48. Thereafter cropping steadily declined, the average yearly yield per tree in 1955-56 being only 55 lb. as compared with 125 lb. at the peak.

The figures in Tables VII and VIII do not refer to all the trees, because in the winter of 1943-44 half of them were removed. For the purposes of these Tables there are throughout six blocks of only four trees each, with two trees missing. All figures relate to variation of trees within a block.

Conference pear.

This trial was arranged in four blocks, each of six trees. In two blocks the rootstock was Quince A and in the other two Quince B ; for each rootstock one block comprised all inside trees and the other all outside ones. One-year-old trees had been planted in January 1921 and bore their first appreciable crops, 2·2 lb. and 2·6 lb. per tree in 1927 and 1928 respectively. Crops in 1929 slightly exceeded 28 lb. per tree. In the frost years of 1935 and 1944 crops were not markedly low, but they were so in 1937 and 1946 after heavy crops in 1936 and 1945. The frost of 1941 appears to have made cropping patchy.

Notes on the Tables.

In all the Tables the results of calibration will be presented as the percentage reduction in the error variance (Parker, 1942). The same figure represents the percentage reduction in the size of trial made possible by calibration, the accuracy being held to a constant figure. It does not show the reduction brought about in the coefficient of variation ; this will be less and is given by the formula

$$100\left[1-\sqrt{1-\frac{B}{100}}\right]$$

where B is the figure given in the Table. Hence, if the error variance is reduced by 50%, the coefficient of variation will be reduced by 29%.

CALIBRATION BY CROP RECORDS ONLY.

First it may help to re-examine some of the results already given by Parker (1942). In Table I are set out some figures selected from his Table III. The trees had been planted in 1917, and the figures relate to the total crop in three four-year periods, 1928-31, 1932-35, and 1936-39, and indicate the percentage of the variation that can be accounted for by the various calibrating quantities. Of these there were sometimes one, sometimes two, and sometimes four.

TABLE I.

Percentage reduction in error variance of crop brought about by covariance on earlier crops; oranges.

Number of calibrating quantities	Years used for calibration	1928-31	1932-35	1936-39
A One	1926-27	45	30	25
B Two	1926, 1927	45	29	38
C One	1924-27	42	23	23
E Four	1924, 1925, 1926, 1927	48	34	36
F One	1922-27	40	16	20

Corresponding figures for the three East Malling trials are given in Tables II-V, the two sets for the Lane's Prince Albert apples referring to different ages. No single figure can be given for assessing significance levels because of the differing numbers of calibrating quantities, but in Tables II, III and V a reduction of 19-22% in error variance is significant at the level $P = 0{\cdot}05$, 30-35% at $P = 0{\cdot}01$, and 44-50% at the level $P = 0{\cdot}001$. In each instance the lower limit applies for one calibrating quantity, the upper for four, and intermediate values for two or three. For Table IV the limits are 9½-10 ($P = 0{\cdot}05$), 16-17 ($P = 0{\cdot}01$), and 24-26 ($P = 0{\cdot}001$).

It first appears that the straightforward method of just using single covariance on the crop of the last two years of the calibrating period (Line A of Tables I-V) is

TABLE II.

Percentage reduction in error variance of crop brought about by covariance on earlier crops; Lane's Prince Albert apple (younger).

Number of calibrating quantities	Years used for calibration	1935-38	1939-42	1943-46
A One	1933-34	72	55	19
B Two	1933, 1934	79	64	15
C One	1931-34	59	47	15
D Two	1931-32, 1933-34	71	53	20
E Four	1931, 1932, 1933, 1934	79	63	5
F One	1929-34	35	23	5
G Three	1929-30, 1931-32, 1933-34	71	59	12

surprisingly successful except with the Cox's Orange Pippin apples, where 1937 and 1938 were both poor years. Further, with the Conference pears this method would have been successful even if eight years had elapsed between calibration and starting the experiment.

Increasing the calibrating period to four years (Line C) or six years (Line F) was of dubious advantage. For the Conference pears, which exhibited a remarkable continuity of cropping pattern, the longer periods appeared to be advantageous, especially when there was a delay before applying treatments. Similarly, the Cox's Orange Pippin apples were better calibrated when the heavy 1936 crop was added to the light crops of 1937 and 1938. The further extension to six years at least did no harm. With the oranges and the Lane's Prince Albert apples the shorter periods were better, or at all events no worse.

Another device that might be considered is to divide the calibrating period and then, instead of using single covariance on the total crop, to use multiple covariance on the crops in the various sub-periods. Although the arithmetic would thereby be much increased, the suggestion is an attractive one ; a field may have characteristic cropping patterns for dry years, wet ones, warm ones, cold ones, windy ones, etc., and it is unlikely that these will occur with equal relative frequency in the calibrating

Table III.

Percentage reduction in error variance of crop brought about by covariance on earlier crops; Lane's Prince Albert apple (older).

Number of calibrating quantities	Years used for calibration	1943-46
A One	1941-42	50
B Two	1941, 1942	47
C One	1939-42	45
D Two	1939-40, 1941-42	47
E Four	1939, 1940, 1941, 1942	51
F One	1937-42	46
G Three	1937-38, 1939-40, 1941-42	45

Table IV.

Percentage reduction in error variance of crop brought about by covariance on earlier crops; Cox's Orange Pippin apple.

Number of calibrating quantities	Years used for calibration	1939-42
A One	1937-38	6
B Two	1937, 1938	13
C One	1936-38	50
D Two	1936, 1937-38	49
E Three	1936, 1937, 1938	47
F One	1933-38	58
G Three	1933-34, 1936, 1937-38	55

TABLE V.

Percentage reduction in error variance of crop brought about by covariance on earlier crops; Conference pear.

Number of calibrating quantities	Years used for calibration	1944-47	1948-51	1952-55
A One	1942-43	86	69	59
B Two	1942, 1943	87	67	59
C One	1940-43	90	77	70
D Two	1940-41, 1942-43	90	78	74
E Four	1940, 1941, 1942, 1943	94	76	72
F One	1938-43	92	75	75
G Three	1938-39, 1940-41, 1942-43	91	78	79

and experimental periods. If then the years of the calibrating period are taken separately and each is given a weight according to its relevance to the experimental period (which in effect is what happens in a multiple analysis of covariance), better results might be expected. In the event little advantage was gained. Thus, comparing Lines B and A in the Tables, or Lines E, D and C, or Lines G and F, there are not many examples of increased reduction of error. With the oranges (Table I), dividing the period gave an improvement when there was a delay after calibration, while with Lane's Prince Albert apple there was an improvement when there was not a delay. Divided periods were never much less effective than undivided ones, but their advantage is problematical and not worth the arithmetic.

To sum up, calibration by crop over the shortest period, i.e. two years, and by the simplest statistical technique, i.e. single covariance—the results of which are set out in Line A—was in general as good as its rivals, and is accordingly recommended.

CALIBRATION USING RECORDS OF BOTH CROP AND TRUNK GIRTH.

Parker (1942) makes it clear that with his oranges measurements of trunk girth were of little use in calibrating crops, but this is often not so for apples (Pearce, 1949). Accordingly, the effectiveness of the four following quantities were compared :

x, crop in the previous two years ;
x', total crop since planting ;
y, increment of trunk girth in the previous two years ;
y', trunk girth at the start of the experimental period.

Results are set out for the East Malling trials in Tables VI-IX, Table VIII being supplementary to Table VII to cover more effectively the period round tree thinning and the damaging frosts.

The total crop from planting was not in general as effective a calibrating quantity as was crop over the preceding two years, a result that is not surprising in view of those already presented, though with Conference pear the continuity of the pattern of cropping was such that at times the total crop was actually the better. On the other hand, the actual girth was usually better than the two-year increment. Here the Cox's Orange Pippin apples came near to providing some exceptions.

Table VI.

Percentage reduction in error variance of crop in two-year periods by covariance on crop and trunk-girth data; Lane's Prince Albert apple.

Period	Coefficient of variation	Calibrating quantities				
		Two-year crop=x	Total crop	2-year girth increment	Total trunk girth=y'	x and y'
1927-28	40	0	1	0	0	0
1929-30	23	28	26	2	27	44
1931-32	24	27	26	15	27	36
1933-34	19	16	7	32	45	44
1935-36	16	59	18	2	41	61
1937-38	27	54	60	4	40	57
1939-40	21	71	50	10	23	70
1941-42	31	56	55	0	30	60
1943-44	34	46	22	14	17	43
1945-46	33	56	34	0	5	53
1947-48	13	0	0	0	0	0
1949-50	18	62	0	4	25	60
1951-52	26	52	0	12	43	59
1953-54	15	0	0	0	0	0
1955-56	20	0	14	26	0	0

Significance of reductions in error variance for all but the last column:

	P=0·05	0·01	0·001
1927-46	19	30	44
1947-56	36	54	72

The broken line indicates the thinning of the plantation and the reduction in the number of trees from 24 to 14.

Table VII.

Percentage reduction in error variance of crop in two-year periods by covariance on crop and trunk-girth data; Cox's Orange Pippin apple.

Period	Coefficient of variation	Calibrating quantities				
		Two-year crop=x	Total crop	2-year girth increment	Total trunk girth=y'	x and y'
1933-34	21	7	33	20	17	28
1935-36	20	53	44	0	9	50
1937-38	34	6	18	0	42	40
1939-40	17	32	28	43	49	47
1941-42	18	0	0	3	0	0
1943-44	23	4	14	2	35	38
1945-46	27	40	33	17	45	51
1947-48	21	22	24	0	59	57
1949-50	32	34	26	25	59	56
1951-52	26	46	30	25	51	51
1953-54	34	56	38	32	57	64
1955-56	33	38	49	51	56	54

Significance of reductions in error variance for all but the last column: P=0·05, 23; P=0·01, 37; P=0·001, 53.

TABLE VIII.

Percentage reduction in error variance of crop in two-year periods by covariance on crop in the preceding two years; Cox's Orange Pippin apple.

Period	Coefficient of variation	Percentage reduction	Period	Coefficient of variation	Percentage reduction
1934-35	23	33	1940-41	23	12
1936-37	19	73	1942-43	23	10
1938-39	22	31	1944-45	28	4

Significance as in Table VII.

TABLE IX.

Percentage reduction in error variance of crop in two-year periods by covariance on crop and trunk-girth data; Conference pear.

Period	Coefficient of variation	Calibrating quantities				
		Two-year crop $=x$	Total crop	2-year girth increment	Total trunk girth $=y'$	x and y'
1930-31	24	25	9	11	33	51
1932-33	26	44	33	0	49	63
1934-35	30	28	24	2	45	45
1936-37	20	37	41	29	67	67
1938-39	29	65	84	24	60	67
1940-41	30	85	84	7	52	84
1942-43	26	78	72	0	40	78
1944-45	30	78	84	14	56	81
1946-47	30	82	88	2	52	82
1948-49	33	82	78	0	39	81
1950-51	37	29	41	0	64	63
1952-53	34	44	86	33	41	45
1954-55	20	12	19	0	38	35

Significance of reductions in error variance for all but the last column: $P=0{\cdot}05$, 19; $P=0{\cdot}01$, 30; $P=0{\cdot}001$, 44.

Comparing x, the previous two years' crop, and y', the total girth, it appears that when one is good the other is commonly at its worst. Thus in Table VI, x was not very effective for 1933-34, but y and y' were better than usual. In 1931 the crop had failed and this had not been compensated for by a heavy crop in 1932, so in 1931-32 the principal activities of the tree had been in growth and it was the growth records that calibrated more effectively. In 1935, and again in 1941, crops were light but the following years redressed matters, and x was reasonably effective for calibrating the following two-year periods.

The interpretation of Tables VII and VIII is difficult, especially before the trees were thinned. Thus, the period 1935-36, in which there was no crop in the first year and a heavy one in the second, was low in variability and gave a good correlation with previous cropping performance but not with tree size. Six years later, in 1941-42, rather similar circumstances obtained, though the crop loss in 1941 was not nearly as great as in 1935, and again variability was low but there was no correlation with

previous crops. In 1938-39 the correlation was intermediate in value. The highest correlation with earlier yields was that found in 1936-37, where the period contained the heavy crop before a frost and the low one following it ; no counterpart is to be found in 1942-43, 1939-40 being intermediate. In the years preceding thinning in 1943-44, the trees must have been getting crowded and this may explain the general tendency for patterns of cropping to be lost, correlations becoming low. Certainly, in the effects just noted, the results are initially clear-cut and become progressively less so although reasonably similar conditions recur.

One interesting period is 1937-38 ; 1937 was a poor cropping year and there was a frost in 1938. Hence cropping was low and, as is shown in Table V, variability was high. When this period was used for calibration, i.e. in 1939-40, the correlation is with girth increment rather than with the two-year crop, girth increment having been the more marked activity of the plants in the calibrating period.

After thinning, the immediate tendency was for crops to be correlated with tree size, as measured by trunk girth, rather than with previous crops. From 1947-48, crops were falling and again correlations were with the girths rather than with the crops; over this period, where trunk growth was the more marked activity, the two-yearly girth increments were useful. Also, with decreasing crops, the coefficient of variation rose to an awkwardly high level.

In Table IX are shown the corresponding figures for the Conference pears. In the main, variability was high but the calibration remarkably successful. For a time, approximately 1940-49, cropping patterns were extremely uniform and changed so little that calibration by the two immediately preceding crops and by the total of previous crops were as good as one another. The association of cropping with tree size was not as close ; it appears that the cropping pattern was not the result of some trees being permanently larger. Possibly this result may arise from the trees having always been crowded. It is true that, with the Cox's Orange Pippin apples, crowding appears to have had the effect of reducing all correlations, but supposedly after a time the situation settles down, and those trees that have established the most competitive root systems and have secured for themselves a good share of the light will continue to crop better, and perhaps make more extension growth without necessarily increasing their trunk girth to match.

The effectiveness of the two-year girth increment for calibrating the crop in 1952-53 is probably due to the low and variable crops of 1950-51 being accompanied by a large increase in development of girth. Its effectiveness in 1936-37 and 1938-39 is harder to explain ; the largest girth increments were in 1930-31 and 1932-33, but these do not appear to be reflected in the calibration of crops in 1932-33 and 1934-35, though a rather large one in 1936-37 appears to have had an effect on the calibration of crop in 1938-39.

Towards the end of the time covered by this study, correlations tended to fall off and the crops of 1954-55 suddenly gave a reasonable level of variability.

Since there appears to be an antagonism between x and y'—the best two calibrating quantities, one being at its best when the other is at its worst—an additional column has been added to Tables VI, VII and IX to show the result of double covariance on the two of them. In general, the results are encouraging.

From Table VI it appears that calibration, as measured by the last column, is sometimes most effective when least needed, i.e. when the coefficient of variation is low anyway, but this does not appear to apply generally.

DISCUSSION.

One clear conclusion from this work is that relations between current crop measurements and previous observations are very complex. Nevertheless, certain useful conclusions have emerged.

Whether crops are better adjusted by previous crops or by trunk measurements appears to depend upon circumstances. With Parker's orange trees, trunk girth was no good at all ; with the Lane's Prince Albert apples, previous crops were usually the better, but on one occasion failed when the girth was at its best ; with the Cox's Orange Pippin apples, girth was usually the better, but on one occasion failed when the previous two-year crop proved especially satisfactory ; with the Conference pears, crop in the previous two years was usually best of all, but again there were occasional lapses when the girth would have been the better. In these circumstances, with apples and pears, the proposal to employ double covariance on both the girth at the beginning of the experiment and crop in the preceding two years has much to commend it. When trees are young there are instances when it would be more effective than single covariance on either quantity alone ; with older trees, it gives results about as good as the better of the two single quantities. On the other hand, double covariance demands much more computing labour.

If the experimental period is preceded by a period of poor and irregular yields, calibration by previous crops is unlikely to be very effective, and in these circumstances the trunk girth is often at its best. Similarly, in the later years of the trial of Cox's Orange Pippin apples, when crops were declining, the girth was to be preferred. Again, with young trees girths are often better. Thus, in general, crop records are better when the trees have been cropping to capacity ; otherwise, girth records are more effective.

When crop records alone are used for purposes of calibration, only with the Conference pears have long calibrating periods proved advantageous. In that instance the cropping pattern was so stable that often the total crop since planting was better than that in the previous two years, but in general this was not so with old trees. Also, despite a certain amount of success with the oranges, the method of dividing the calibrating period and using multiple covariance did not appear to be better than taking the total crop in the calibrating period and adjusting it by the method of single covariance.

The thinning of a plantation before starting an experiment may well be considered. The results with Cox's Orange Pippin apples and Conference pears suggest that the development of crowded conditions can cause rapidly changing cropping patterns that make calibration difficult. However, the apples never cropped well even after they were thinned, and there may have been some special circumstances. Also, thinning a plantation can make calibration difficult for a while, so the application of treatments should if possible be delayed until conditions have settled down. Against this, it should be recalled that, after thinning the Lane's Prince Albert apples, there was little need of calibration because they became so uniform.

Finally, given good calibration, by how much can the error of an experiment be reduced? Using the double covariance method, it appears that the variance, and consequently the size of an experiment, can usually be reduced by a half or more, an improvement on the figure of a third given previously (Pearce, 1949). This underlines the usefulness of the approach. Of course, an experimenter is often interested in many

quantities beside crop, and there is not much evidence how they may be calibrated ; also, an experiment must be large enough to provide adequate information about all the quantities under study, and it will not always suffice to use only enough material to determine the crop records. However, these are often among the most difficult and the effective reduction of their variability is of some importance.

SUMMARY.

Data are examined from two apple trials and one pear trial over periods of 25-30 years to determine what measurements of previous performance, whether of trunk girth or of cropping, will be most associated with the crops of an experiment started when trees are already established. With apples and pears, crop in the two years preceding the start of an experiment is often very effective, and so is the trunk girth at the start. Usually, however, if one is effective the other is not, so the method of double covariance is suggested for making the adjustments. When this is done the error variance may be halved. Studies are made of other means of using past crop records for this purpose. Results are compared with those of a previously published investigation by Parker (1942) on oranges.

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THE RÔLE OF SECONDARY INFECTIONS IN THE SPREAD OF APPLE MILDEW (*PODOSPHAERA LEUCOTRICHA* (ELL. AND EV.) SALM.)

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THE work of Woodward (1927) and of the present writer (Burchill, 1958*a* and *b*) has established that the perennation of this obligate parasite is solely by overwintering mycelium established within buds during the previous summer. The contribution made by individual buds to the potential inoculum available the following spring depends on whether the bud is borne laterally or terminally on an extension shoot, or is a fruit bud on a short spur. The majority of fruit buds have only a brief period of susceptibility to infection, limited to May and June. Terminal buds, however, can be infected throughout the period of shoot extension, which may continue until September. Lateral buds individually are susceptible only for approximately a month after initiation but, as they are formed successively through the growing season, they have collectively a long period of susceptibility.

After winter dormancy the fruit buds are the first to open and, if mildewed, they provide a source of conidial infection in the period April-May. The terminal buds open approximately three weeks later and, if infected, they produce extension shoots on which mildewed leaves arise in succession as long as growth of the shoots continues. The axillary buds carrying overwintering mildew provide a relatively limited supply of conidia since they produce only a few mildewed leaves which are soon shed.

The mildew present at bud break on leaves, flowers and shoots constitutes the "primary infection phase". Conidia from these sources may attack healthy leaves during the whole growing season and the resultant infections represent the "secondary infection phase".

The importance of this latter stage in the life history of the fungus has been the subject of much comment. Woodward (1927) claimed that such infections played only a limited rôle in the spread of the disease, attributing the yearly increase in bud infections solely to the natural increment from the growth of infected buds into extension shoots furnished with axillary buds infected *ab initio*. Later, however, Petherbridge and Dillon Weston (1929) concluded that secondary infections were of more significance in the spread of the disease than was at first assumed. Furthermore, Müller (1955) demonstrated that the prevention of secondary infections, which he found could occur at any time from petal fall until the termination of shoot growth, was the only means of controlling mildew. Aerts and Soenen (1955) also challenged Woodward's views and concluded that secondary infections were mainly responsible for new infections of the buds and were essential to the spread of the disease.

The results of an investigation into the rôle of secondary infections in the life history of the fungus are described below.

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Materials and methods.

Thirty bush trees of the variety Cox's Orange Pippin on Malling II rootstocks planted in 1935 in a 30 ft. × 30 ft. quincunx were used to study the distribution and spread of the disease in the field. Selected branches from a further twenty trees planted similarly were mapped during a period from May 1955 until September 1957. On these individual branches the position of leaves, shoots and blossom trusses was noted, and monthly detailed examinations and records were made of the spread of established infections and the initiation of new attacks. Selected trees of the same variety from a three-acre grass orchard laid down in 1947-48 on M.II rootstocks, with the varieties Laxton's Superb and Winston as pollinators, were used in comparing the effects of different pruning systems on mildew incidence.

RESULTS.

Experiment 1.

Relationship between development of secondary infections and weather conditions.

Observations on the initiation of new infections show that the youngest fully unfolded leaf on the extension growth is the most liable to mildew attack, resistance increasing progressively as the leaves mature. In the field new infections are invariably confined to the lower surface of the leaf, particularly in the region of the mid-rib. At an early stage in attack, the presence of the fungus causes upfolding of the leaf margins ; later, as the infection spreads, the leaves become brown and brittle.

The incidence of new secondary infections was low during periods of prolonged rainfall. Experiments by Woodward (1927) and the author (1958*b*) on the germination requirements of conidia demonstrated the poor germination of spores present on a surface bearing free water. This may, therefore, be one of the major contributory factors to the low incidence of new infections during wet seasons.

Records of the weather conditions and of the initiation of new infections in 1956 (Table I) show that in May, which was exceptionally dry, secondary infections were frequent, and similarly in late June and early July. Heavy rain in August restricted mildew spread but, with a return to drier conditions in September, there was a corresponding rise in the number of new infections, which brought the total infection for the season to 51% of the shoots on the recorded extension growths.

Table I.

Increase in mildew infections in 1956.

Month	Rainfall, 1956		New infections; % of new shoots infected each month	Accumulative infection; total % of shoots infected
	Inches	% of monthly average		
May ..	0·50	19	20	20
June ..	2·78	132	8	28
24th June–15th July	1·00	—	12	40
August ..	7·99	219	3	43
September	3·55	112	8	51

In 1957 conditions were similar, the early months being dry and favouring infection, whereas the later months, July to September, were wetter than normal and therefore unfavourable to mildew increase. In 1958 May and June were unsettled, with an above-average rainfall, and again the low incidence of secondary infections was noticeable.

The effects of wind and light on the incidence of the disease were difficult to assess but, from records of distribution in the field, infection was most severe on that side of the tree sheltered from the prevailing wind and from direct sunlight.

EXPERIMENT 2.

Rôle of secondary infections in perennation.

In addition to the mapping of branches a further 910 extension shoots were examined at fortnightly intervals throughout the summer of 1956. In the following spring a re-examination was made to determine the effects of the previous year's infection on the carry-over of the disease into 1957 (Table II).

TABLE II.

Origin of mildew infection on 910 shoots.

September, 1956		Spring, 1957	
Condition of parent shoots	% of total	Condition of new extension growths	% of total
Primary infected	4·5	Healthy	0·0
		Mildewed	1·1
		Dead	3·3
Other shoots			
Healthy	18·5	Healthy	87·9
Carrying secondary infections only	77·0	Mildewed	7·7
		Dead	0·0
Total mildewed shoots (primary infections)	4·5		8·8

The results indicate that of the 8·8% mildewed extension shoots (primary infections) emerging in 1957 only 1·1% had arisen from shoots primarily infected the previous year and 7·7% from shoots that bore only secondary infections of the leaves in 1956. The terminal buds which gave rise to the latter shoots had been infected later in the season by extension of the fungal mycelium from the infected lamina, along the petiole and into the bud (Burchill, 1958*b*). The large proportion of dead shoots (3·3%) found in 1957 was due to infection of the terminal bud being so severe that often this bud and several inches of the shoot were killed.

It is concluded that the carry-over of the fungus is predominantly dependent upon the establishment of secondary infections on the leaves, particularly the terminals, and subsequent spread of the disease from the infected lamina along the petiole, so as to infect the bud.

Experiment 3.

Importance of late summer secondary infections of terminal buds.

It has been previously shown (Burchill, 1958*a* and *b*) that many of the late season secondary attacks on terminal leaves result in infection of only the terminal bud. Such infections often cause no modification of the bud and, although most diseased buds are dwarfed, terminal buds infected at this time are normal in appearance. This raises a pruning problem in that, although spur-pruning ensures the annual removal during the dormant season of most healthy and diseased terminal buds, the renewal and regulated systems allow for the removal of only obviously mildewed terminal buds. Thus late-infected and therefore apparently normal terminal buds remain to carry over inoculum to the following spring (Burchill, 1958*a*).

In order to test this observation a further experiment was made in the winter of 1957-58 to determine the effect on perennating mildew of tipping leader growths. Twenty-four trees of equal girth and size from two selected plots, A and B, were renewal pruned and in addition one inch of each extension growth over six inches long was removed on half these trees. On all trees, however, obviously mildewed buds and shoots were removed during the pruning. At the time of pruning, counts were made of all the shoots remaining on the trees and of those removed. In June 1958 the numbers of mildew infections were recorded (Table III).

It is evident that tipping all leader growths eradicated much of the overwintering fungus and therefore markedly reduced the inoculum potential the following spring.

DISCUSSION.

In mildewed orchards conidial inoculum on shoots and leaves is available from the time the diseased buds first unfold, and from these primary sources succeeding leaves are liable to infection. These progressive foliar infections provide the inoculum for further spread of the disease. In dry weather new infections may occur throughout the season, but wet conditions appear to restrict them.

In the control of apple mildew, the ultimate objective is the protection of buds from infection, thereby breaking this disease cycle. Apart from the costly cutting-out of mildewed twigs there is no established method of preventing infection by eradicating the conidial inoculum. Consequently the principal means of control is by using fungicidal sprays to protect uninfected tissues. It is, however, unlikely that the efficacy of such sprays lies in the deposition of a protectant coating on susceptible buds, for lateral buds, when young, are almost entirely enclosed between the stem and the concave face of the subtending petiole and are thus shielded from spray deposition. Also terminal buds and fruit buds, in addition to being enclosed by leaf bases, are densely invested with hairs, and this adds to the difficulty of providing a protectant covering of the fungicide.

The major effectiveness of fungicide sprays is therefore in checking the establishment and spread of secondary leaf infections. As these infections provide the source of the mycelium that grows down the petiole to invade the bud, it is evident that the prevention of leaf infection indirectly safeguards the buds by eliminating the source of inoculum, not only for the buds but for other leaves also. The limited period of susceptibility of fruit buds makes it possible to obtain good control of this source of overwintering by carefully timed sprays during the post-blossom period (Burchill,

TABLE III.

Results of mildew pruning trial (June 1958).

Plot	Normal pruning in winter, 1957-8				Normal pruning and tipping of shoots longer than 6 in. in winter, 1957-8			
	Shoots > 6 in. per tree (*a*)	Shoots with mildew in June 1958		% infection (*c*)/(*a*)	Shoots > 6 in. pruned per tree (*d*)	Shoots with mildew in June 1958		% infection (*f*)/(*d*)
		Total (*b*)	> 6 in. (*c*)			Total (*e*)	> 6 in. (*f*)	
A	310	47	33	10·32	284	13	3	1·05
	534	160	111	20·78	360	62	17	4·70
	268	69	43	16·04	261	44	9	3·44
	147	46	28	19·04	135	28	8	5·92
	223	56	31	13·90	288	45	9	3·12
	249	42	24	9·63	314	11	0	0·0
	Total 1,731	*420*	*270*	*15·59*	*1,642*	*203*	*46*	*2·80*
B	177	12	5	2·82	167	7	0	0·0
	218	86	56	25·68	261	30	4	1·53
	283	51	38	13·42	254	25	6	2·36
	234	66	36	15·38	243	17	3	1·23
	159	130	67	42·13	185	43	6	3·24
	123	45	26	21·13	146	16	4	2·73
	Total 1,194	*390*	*228*	*19·09*	*1,256*	*138*	*23*	*1·82*

1958*a*). However, with the continued production of new foliage and the long period of susceptibility of the terminal bud, spray applications in general apparently do no more than interrupt the flow of infection. Fungicidal sprays extending well into the summer would reduce secondary infections and subsequent infection of terminal buds but such measures are unlikely to be economic.

Finally, experiments have shown that, as an adjunct to spray treatments, the amount of fungus perennating in a tree can be reduced by the removal of all the terminal buds, the major sites of overwintering infection. The regular use of such a drastic method of control, inasmuch as it would increase production of extension shoots, would militate against proper tree management and might jeopardize tree shaping and crop production. However, a limited application of this method, or even spur-pruning, might be justified in areas of high mildew intensity. Elsewhere, a suitable programme of post-blossom sprays, combined with cutting-out of all visibly mildewed shoots in winter and of diseased blossom trusses and extension shoots in the spring, is the most practicable programme that can at present be recommended.

SUMMARY.

The infection of leaves in the field and the effects of the host and of climatic conditions on the subsequent spread of apple mildew are described. During periods of low rainfall in the summers of 1956 and 1957 new secondary infections increased, but with a higher rainfall there was a corresponding reduction in the number of such attacks. Records of the spread of secondary infections in the field have provided quantitative data establishing that such infections have a significant bearing on the amount of mildew arising in the following season as primary infection.

The rôle of the late infection of terminal buds in the overwintering of the fungus is discussed in relation to recent changes in pruning techniques. The tipping of all leader growths over six inches long reduced mildew level in the early summer of the succeeding year to approximately 10-20% of that on trees not thus treated.

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AN APPROACH TO THE STUDY OF YEARLY AND OTHER VARIATION IN CROP YIELDS

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It is an accepted practice in field experimentation that treatments must be tested for a number of years if the results are to be firmly enough established to justify recommending some of the treatments for practical use. The reason for this is that the effects of years are frequently greater than those of the treatments, and hence the experimenter is in the position of having some important factors influencing the growth of the crop outside his control. The large size of the year effects usually implies that there will be considerable interactions between treatments and years ; if the basis of these interactions is not known, there seems to be little alternative to regarding the year effects as a random sample from some population of years, and making inferences accordingly. This procedure leads to the sort of analysis developed, for instance, by Cochran and Cox (1957), and expressed in terms of variance components. The experiment must be carried on sufficiently long for the average treatment effects to be clearly distinguishable, using the treatment × years mean square as an error term. The variance component model, however, can only be regarded as a first step since it treats as random, i.e. as inexplicable and unpredictable, something which is having a major effect on the crop yields. The value of any series of field experiments would be greatly increased if models could be developed which were capable of accounting for these yearly differences in treatment response. Yearly differences and treatment × year interactions, instead of being regarded as unpredictable, would then be seen as effects of the particular years during which the experiment was done, and the prediction of treatment response in other years would thereby become possible.

We shall consider the construction of such a model when measurements over the whole growth of the crop are available and not merely the final yields; we shall thus be concerned with possible relationships between the growth of the crop and the climatic and edaphic factors in the environment. This has been the subject of a number of previous investigations. Thus Clements (1951) grew sugar cane at different times of the year and in different places, recording the various climatic factors and the growth of the crop simultaneously. A multiple correlation technique was then used to show that soil moisture, temperature and solar radiation were all highly correlated with various aspects of growth. Using a basically similar technique, Geslin (1954) correlated the growth of wheat leaves over 24-hour periods with temperature and global radiation when soil moisture supply was non-limiting. He emphasized that, to describe the growth of wheat, it was necessary to postulate the simultaneous action of temperature and light. Ottosson (1958), working with the pea crop, has carefully differentiated between the effects of a climatic variable on growth and on development, whilst many workers have related the development of the pea plant in the field to temperature by the use of phenological data, e.g. Ferguson (1958).

Thornthwaite (1952) and Higgins (1952), however, using a new technique, have measured the effect of climate as a whole on the development of the pea plant. By using the water loss from a plant as an integrated measure of the environment, Thornthwaite (1952) has defined the " development unit " of a plant as the amount of development that will occur while a unit amount of water is being transpired. Penman (1956) has related growth (increase in dry weight) to accumulated potential transpiration.

In some crops the growth, in any one year, is predominantly vegetative (e.g. carrots, cabbage) whereas in others sexual reproduction is an integral part of cropping (e.g. peas, beans). As a first step we have considered the growth of crops of the former type which is probably simpler in character ; this paper describes a possible approach to the interpretation of year-to-year and inter-site variation in such crops, based primarily on the idea of using a " time " scale, derived from meteorological measurements, as an index of growth conditions. Such a scale would, for instance, enable growth curves for a given treatment in different years to be superimposed, so that variation in yields between years—represented by different degrees of extension of the same curve—would be accounted for in terms of variation in the duration and quality of the effective growing weather (i.e. the integral over the growing period of the climatic variables used as the time scale). The idea could be extended to the interpretation of treatment × year and treatment × sites interactions. Some complications caused by the occurrence of temporary checks to growth from which recovery is complete are also discussed.

The hypothesis outlined above has been tested on growth data obtained for carrots and cauliflowers. The work on cauliflowers has been described by Salter (1960) and it is hoped to publish the results obtained with carrots at a later date.

The general development of the theory begins with the simplest case of exponential growth under a regular environment ; we then consider a suitable modification of the growth equation to describe limited growth, and the complications caused by non-additive effects in an irregular environment. Finally we discuss possible uses of the method and compare the assumptions with those of other methods for correlating growth with environmental factors.

Growth in a regular environment.

The most general equation for describing the growth of a part, or the whole, of a plant would embody the initial internal variables in the seed at time $t = 0$, and the relevant external variables from that point onwards. Let us write $x_1 \ldots x_n$ for the n relevant internal variables and $\theta_1 \ldots \theta_m$ for the external m variables at time t, then the most general formulation would take the form

$$W(t) = f(x_1 \ldots x_n, \theta_1 \ldots \theta_m)$$

where $W(t)$ is the weight at time t, and f is some function of all the internal variables and external variables to date. To obtain a practical simplification of this general formulation we consider first early growth, which, from data for many species, we know to be approximately exponential, i.e. of the form $W(t) = W_0 e^{kt}$. We shall interpret this equation in its differentiated form, i.e. as $\frac{dW}{dt} = kW$, assuming this to mean that absolute growth rate is jointly proportional

to existing weight and to a factor k which is a function of the external environment and of internal limiting factors.

We consider, first, growth in an environment which we shall call *regular*. In a regular environment external factors affecting growth either show a steady unidirectional trend with time, or fluctuate with constant frequency and amplitude. In particular, soil nutrient supply for unfed pot plants may be expected to be of the first type. Light, of course, is the most obvious example of the second type; another is water supply under a regime where water status is restored to field capacity when a certain soil moisture tension has been reached. A constant level of any given factor is a special case of either type. W is assumed to be measured at about the same position in each cycle of the varying factor or factors. Suppose now that one of the external factors in a regular environment, say light intensity (I), is altered experimentally and that the varying levels of I produce different k's related to I by some function $k = f(I)$. It follows then that, if we replace time t by a time scale defined by $\tau = \int f(I)dt$, the growth equation for all treatments becomes $\frac{dW}{d\tau} = W$. This is to say no more than that growth is exponential and that $k = f(I)$. If several external factors, $\theta_1, \ldots, \theta_m$, are varied together and we find that $k = f(\theta_1 \ldots \theta_m)$, then similarly the use of a scale $\tau = \int f(\theta_1, \ldots, \theta_m)dt$ will cause all the growth curves to be superimposed. Thus Milthorpe and Newton (1959), studying the growth of cucumber, found that when light intensity (I) and duration (d) were varied jointly, growth was very largely a function of their product $R = Id$. In this case a time scale based on one variate, R = total incoming radiation, would be adequate to produce coincidence of the growth curves.

Most crop plants are not harvested until they have passed the exponential period of growth and have entered the period when the relative growth rate starts to fall. To describe the growth to maturity we need some amendment to the simple exponential relation $W = W_0 e^{kt}$. A frequently used form is the logistic curve which satisfies the differential equation $\frac{dW}{dt} = kW(1 - W/A)$ where k and A are constants.

One derivation of this equation assumes that a factor necessary for growth is present initially in some finite amount and that it is progressively used up by the plant. This is certainly an over-simple view of the complex processes of plant growth, yet it is surprising how often growth of a type very similar to the logistic form is encountered. Another derivation, which we believe to be new, uses the idea that plant growth is limited by the shading of old leaves by newer ones, and leads to a similar type of equation. This argument rests on two assumptions : (i) that relative growth rate is a linear function of log. light intensity and (ii) that Beer's law holds for light penetrating plant foliage, that is, intensity falls off exponentially with weight of material passed through. The justification for (i) (which must break down both for very low and for very high intensities) is empirical (see Blackman and Black, 1959, for examples), while (ii) is based on an analogy with the passage of light through semi-transparent media. Writing R for the radiation reaching a point P, x units below the apex and having a weight of foliage w per unit area above it, and R_0 for the radiation at the apex, then from (ii) $\ln R = \ln R_0 - \lambda w$. If δu is the weight of an element of tissue at point P then from (i)

$$\frac{1}{\delta u}\frac{d}{dt}\left(\delta u\right)$$
$$= \alpha + \beta \ln R$$
$$= (\alpha + \beta \ln R_0) - \lambda\beta\dot{w} \text{ from (ii)}$$
$$= k - Bw, \text{ say.}$$

Therefore the total increment of growth dW, integrating over the whole plant, is given by

$$\int \delta u = dt \int (k - B\,w)\delta u$$

so that

$$\frac{dW}{dt} = kW - B\int w du$$

For the special case where the density ρ of foliage is constant and the canopy horizontal, we have $w = Cx$, where C is some constant, and

$$\int w du = C\rho \int a x dx$$

where a is the cross sectional area at depth x. For a plant growing in 3 dimensions without change of shape, $a \propto x^2$ and $W \propto x^3$, so that $\int w du \propto W^{4/3}$. For plants growing in 2 or 1 dimensions the integral is proportional to $W^{3/2}$ and W^2 respectively.

This last integral leads to the logistic equation. The others lead to an equation of the form

$$\frac{dW}{dt} = kW - BW^{1+\phi} \qquad (1)$$

where ϕ takes a value between 0 and 1. This equation has the solution that W^{ϕ} is a logistic variable, i.e. we can rewrite it in the form

$$\frac{d}{dt}\left(W^{\phi}\right) = k\phi W^{\phi} - B\phi\,(W^{\phi})^2$$

The assumption that ρ is a function of x only and that cover is complete also leads to the logistic equation. In general the special assumptions about the constancy of density will not be exactly true, but it seems reasonable to assume that the integral $\int W du$ can be approximated by some power of W. (1) has been taken as the growth curve for data on carrots and can be justified empirically in that it gives good fits to a number of different sets of data.

It should be noted that (1) is a special case of a growth equation proposed by Bertalanffy (1957) for animal growth. Without necessarily accepting his identification of the two terms on the right-hand side as representing anabolic and katabolic processes, it seems not unreasonable to regard determinate growth as being the result of two opposing processes, one promoting and the other inhibiting further growth, the two processes being in size allometrically related to total weight at any time. It is not essential to the argument for the use of meteorological measurements as time scales that equation (1) should be exactly true, but only that it should produce a suitable graduating curve for representing the data ; nevertheless it is highly desirable that the parameters in such a curve should be capable of some biological interpretation, even if this interpretation is tentative and over-simplified.

Extension of the model to an irregular environment.

Field crops are grown in irregular environments, and we now consider what modifications must be made to the ideas of the previous section when we are dealing with this situation. If weights of a field crop in the early stages are plotted against time it will usually be found that growth is approximately exponential, but variations in weather will cause changes in k at different times in the same year, and at the same date in different years ; while edaphic factors, varying between sites, will also change k and such changes will be confounded with changes due to varying weather. The simplest model for this situation would be one in which $\frac{dW}{dt} = kW$ as before and k is a function only of the external factors at *that time*. That is to say, relative growth takes place in a series of additive increments, each increment being determined by the external conditions at that time. Equivalently we may say that the past history of growth is summed up by the weight of the plant at any time. If this model were true we could calculate the growth in an irregular environment from knowledge of the growth in the appropriate regular environment, using again a scale defined by $\tau = \int f(\theta_1 \ldots \theta_m)dt$. In practice, however, we know that non-additive effects can be produced by variation of several factors.

These non-additive effects appear to fall into two main classes. The first are long-term effects, usually irreversible in field conditions, such as vernalization or photoperiodic effects controlling the induction of flowering. We are not concerned with this kind of effect in this paper. The second-class of non-additive effects may be called *reversible checks*. Fig. 1 indicates the type of effect meant. Suppose that at time t_0 a check to growth is imposed on a growing plant so that from t_0 to t_1 growth proceeds from X to Y′ instead of from X to Y as it would if the check had not been imposed. Then, if at t_1 the check is removed, growth in the checked plant is more rapid than in the unchecked plant and eventually the checked plant reaches a weight equal to that of the unchecked *at the same time*, t_2. Of course if the check is too severe, complete recovery may become impossible and then the plant will have suffered an *irreversible check*. Data given by Milthorpe (1956) show what is probably a reversible check caused by a period of low temperature, though the data as given do not extend to a time of complete recovery. Owen and Watson (1956) have presented limited data that could be interpreted as a reversible check to the growth of sugar beet caused by drought. Salter (1956) has found a high degree of recovery by cauliflowers from quite severe water stress, suggesting that with milder stress recovery would be complete. A rather different kind of check is that imposed by defoliation ; results of Jones *et al.* (1955) show that up to 50% defoliation at the 4-leaf stage in sugar beet gave little or no effect on the weight of tops or roots at harvest time.

Clearly, factors influencing growth by non-additive effects such as reversible checks cannot provide a suitable time scale for an irregular environment if the irregular fluctuations are at all marked. Thus, if a quantity is to be suitable as a time scale, it must be highly correlated with factors influencing growth in a regular environment and itself produce little in the way of non-additive effects in an irregular environment. It is, of course, a postulate of the general hypothesis that such a suitable quantity exists ; that some success along these lines may be achieved is shown by Salter's (1960) work on cauliflower referred to previously.

The generalization of (1) to an irregular environment involves allowing k and B to be functions of external variables as before. On the additive model we can make k a constant by replacing t by a suitable time scale ; an added complication now arises that we do not know that the same time scale will necessarily reduce B to a constant also. Rewriting (1) in the form $\frac{dW}{dt} = kW(1 - W\phi/A)$ we see that a sufficient condition for this would be for A, which equals the asymptotic value of $W\phi$, to be indepen-

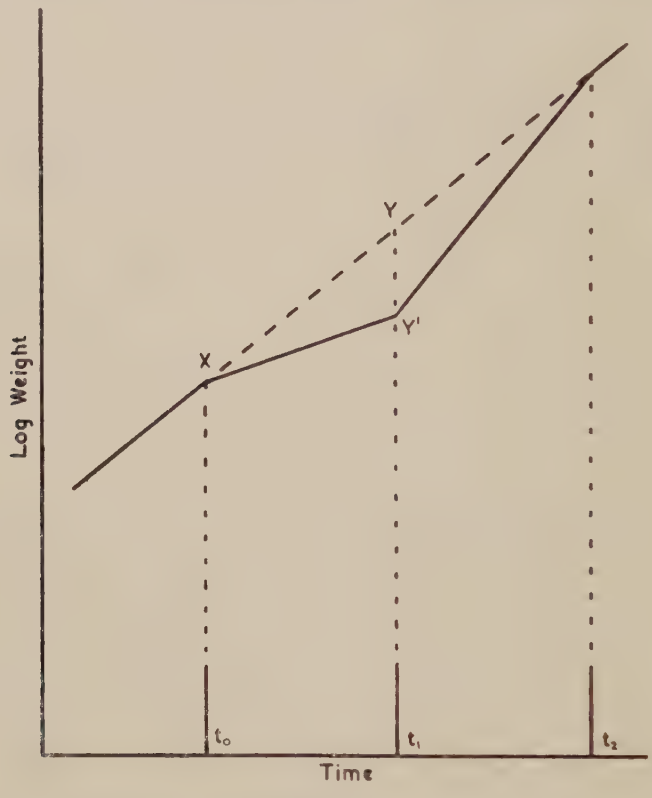

FIG. 1.

Diagram of reversible check to growth. *Solid line*—growth curve with check imposed between t_0 and t_1. *Dashed line*—corresponding growth when no check imposed.

dent of the external variables. Thus we may expect previous arguments to carry over to this more general equation, provided that growth conditions are never so adverse that they prevent the attainment of the final " weight " A, i.e. that all checks are of the reversible type.

Uses of the proposed model.

The main application of a time scale satisfying the conditions discussed above would be to the interpretation of year-to-year and site-to-site differences in long-

term experiments, especially those involving root crops where the final yield is to a large extent determined by the growing season as terminated by the actual lifting, and not by internal, physiological phenomena such as the ripening of grain crops. In particular, trends due to the cumulative effects of, say, manurial treatments might to a large extent be freed from the often considerable variation due to extraneous yearly variation. A further hypothesis that might be tested would be one that climatic and edaphic factors at a site contribute independently to growth so that in the relation

$$\tau = \int f(\theta_1, \theta_2)dt,$$

where θ_1 represents climatic and θ_2 edaphic factors, $f(\theta_1, \theta_2)$ could be split into $f_1(\theta_1)f_2(\theta_2)$, so that for θ_2 constant the use of $\tau_1 = \int f(\theta_1)dt$ would serve to give coincident growth curves for variable θ_1.

In non-irrigated experiments it is likely that soil moisture would behave partly as an edaphic factor and partly as a climatic factor, since periods of high temperature and radiation intensity result in decreasing soil moisture. For soil moisture, therefore, it is unlikely that the independence hypothesis will be satisfactory, and the suggested specialization of the model should perhaps be reserved for irrigated experiments. If such a hypothesis proved adequate as a first approximation, we could begin to interpret not only treatment × year interactions at a given site but also attempt to disentangle the effects of the climate at a given site and the soil characteristics of that site.

A second application of the time scale would be for the study of checks, reversible or otherwise. A suitable time scale should reveal reversible checks more clearly, particularly those caused by temporary water stress. By removing a component of variation due to changes in additive effects, non-additive effects would show up more clearly.

DISCUSSION.

It seems essential in developing methods of growth analysis to allow for internal influence on the growth at any period as well as external influence. Two simple forms for internal factors are obtained by supposing growth in any short period to be a function either of the weight at the beginning of that period or of chronological time. The latter form is essentially that adopted by Glenday (1955, 1959) ; he postulates a growth increment for a given chronological period, external variables being assumed fixed, which is independent of previous weather factors. He shows that for the growth of herbage the model fits satisfactorily ; however it is clear from the form of the growth curve that he is working with a crop in which the absolute growth rate is roughly constant in the period considered. It seems less likely that the model would work satisfactorily for a period of exponential growth, where the growth increment is probably limited by the initial amount of material present. For this reason we have chosen to work with a model where the internal factors are expressed in terms of weight, though this is certainly an over-simplification. A more general model is considered in an interesting recent paper by Skellam *et al.* (1959). Briefly they suppose that the relative growth rate of any organ can be expressed as the product of

two functions, one embodying the " major operative factors " and not containing the time t, the other a function of time which embodies the effect of " minor factors ", In the example on animal growth which they work out in detail, it appears that both the major and minor operative factors are what we have termed internal factors. However, if we suppose in their model that one function depends on internal factors only while the other depends on environmental factors, then equation (1) above when written in the form

$$\frac{1}{W}\frac{dW}{dt} = k(1 - W\phi/A)$$

will be a special case of such a model if ϕ and A are assumed to be structural parameters independent of the environment, while k depends on it. Skellam *et al.* also consider a transformation of the time scale, which is equivalent in (1) to making k a constant. The main difference between their approach and ours, as judged by their example, is that they regard the time scale as a dumping ground for less important internal factors while we regard it primarily as a means of eliminating the effects of a fluctuating environment. In practice there can be little doubt that it will have both functions and that, as Skellam *et al.* suggest, progress will come from a further sub-division of the factors subsumed under the single transformed time scale.

An alternative form of analysis might be based on multiple regression, but it would be necessary to include among the independent variables the initial weight or some function representing internal factors. The difficulty then arises that the regression coefficient of the weight function will itself be a function of the external factors, for reasons discussed above ; thus the system does not seem to be easily reducible to the normal regression model.

The essential feature of a suitable time scale is predictability, as shown by the relative stability from year to year of some or all of the parameters in the growth equation. It is not sufficient that some equation, whether of the multiple regression type or of some other kind, should give a good fit to the data internally, that is to growth within one particular crop ; it must also give repeatable results from occasion to occasion. All the models known to us for connecting growth in plants with environmental factors are of the additive type, that is to say it is assumed that the effect of a given set of factors during some short time interval is independent of the states of these factors at other times. A point to notice is that, if reversible checks are at all common in plant growth in the field, then it may be dangerous to judge the value of an additive model solely on its " internal " goodness of fit, because the independent variables chosen to give a good fit to the additive model are those which happen to fit a non-additive situation. If a fair number of points on the growth curve are available, however, it will often be found that estimates of parameters are much less upset by non-additive phenomena than are residual mean squares about the fitted curve. This constitutes a further reason for taking repeatability as the criterion for successful fitting and may well be an argument for limiting the fluctuations of external factors, such as soil moisture, until we have some insight into the simpler situation.

There is no reason in theory why time scales, not necessarily the same, should not be found for the component processes of growth, such as leaf initiation, leaf expansion, assimilation rate, etc. This development would necessitate, however, far more knowledge about the mutual effects of these processes on each other than is at present available, and can only be seen at the moment as a desirable goal for future work.

SUMMARY.

(1) Difficulties in the interpretation of long-term field experiments caused by the large year-to-year variation in crop yields are discussed and previous work on the subject reviewed.

(2) The idea is put forward of replacing chronological time in the growth equations of vegetative crops by a time scale based on some suitable combination of meteorological factors.

(3) The theory is developed first for unrestricted (exponential) growth in a regular environment, and then extended to restricted growth, using a generalized form of the logistic equation as the basic growth curve.

(4) Complications caused by non-additive effects in an irregular (field) environment are discussed, particularly those of the type which produce reversible checks to growth.

(5) Applications of the model are suggested for the interpretation of treatment × year and treatment × site interactions and for the investigation of reversible checks.

(6) The present model used is compared with others previously proposed for growth analysis, and the view is put forward that repeatability of results is the only sound basis for judging the value of such models. A possible extension to growth components is envisaged.

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BOOK REVIEWS

TREE FRUIT PRODUCTION. By James S. Shoemaker and Benjamin J. E. Teskey. (New York : John Wiley and Sons, Inc. London : Chapman and Hall, Ltd. 1959. Pp. 456, illus. Price 56s.)

It is hard not to be envious of the horticultural students in North America for they are indeed fortunate in the wealth of textbooks available to them. Many of these tend to be of rather restricted value outside the United States and Canada, and some are applicable only to the local conditions of one or two of the States. There have been exceptions, e.g., Chandler's *Deciduous Orchards* and Gardner's *Fundamentals of Fruit Production*, but recent attempts to keep these important and valuable books up to date have not been very successful. Since the textbook that draws attention to the principles underlying each operation has yet to be written in this country, the arrival of a completely new American one devoted to tree fruits obviously deserves special attention, especially as its authors have experience gained in all the chief fruit-growing regions in North America. Interest in the book is intensified by an impressive bibliography, in which references to quite recent publications are plentiful.

All the usual deciduous fruits are given a chapter, with the exception of the relatively unimportant nectarines, quinces and apricots, which are briefly considered together. In addition, a chapter is devoted to so-called " dwarf " apples and pears, which are in fact mainly bush trees on rootstocks of moderate vigour. Another chapter deals rather inadequately with citrus, apparently to ensure that the student is aware of some of the unusual features of this crop. The economic importance of the apple and peach crops is recognized in giving up more than half the book to these two fruits. Within each chapter the distribution of the particular fruit in the U.S.A. and Canada is presented, followed by sections dealing with propagation, varieties, choice of site, planting, manuring, pruning and other operations. Picking, storage and marketing are included but pest and disease control is covered in general principles only. It is surprising that virus diseases have been passed over so lightly, without even a mention of the American Handbook of stone fruit virus diseases.

There is much to commend this book to students in all parts of the world and it deserves to be included in the libraries of all horticultural teaching departments. The instructions are clear, usually accurate and up to date, and well documented. The authors claim to have drawn on research abroad as well as in America but they have included only fifteen references to publications outside North America in a total of over 800. The illustrations are plentiful and on the whole useful, but some have suffered from excessive reduction and poor reproduction. It is a pity that a book that is so useful, in spite of the limitations referred to above, should be priced too highly for most students outside the dollar area, and it is high time that a competitor is produced in the sterling area!

H.B.S.M.

PLANT PROPAGATION : PRINCIPLES AND PRACTICES. By H. T. Hartman and D. E. Kester. (New York : Prentice-Hall, Inc. 1959. Pp. 559, illus. Price $8.75.)

More and more students are giving close attention to the underlying principles upon which the practices and skills of propagators are based. There are already many books on plant propagation dealing with both general and particular aspects of the subject and this new work is a major contribution to this extensive library, the shelves of which are pretty tightly filled ; nevertheless it will certainly shoulder itself a place. The authors, both professors of pomology in the University of California, are familiar with students' needs and in consequence have provided an excellent textbook, clear, concise and taking nothing for granted.

The basic principles and techniques are considered separately in alternate chapters and though this may at first appear to be a means of avoiding trouble for the authors it is remarkably efficient. The eighteen chapters are placed in four divisions : general aspects ; sexual propagation ; asexual propagation ; and the propagation of selected plants. The bulk of the book is taken up with the two great propagation methods ; the first section serves to introduce the subject and provide basic botany and cultivation details. The final section deals with special techniques suited to each of the principal fruit and nut species, ornamental trees, shrubs and climbers, herbaceous perennials and annuals. The two middle sections, five chapters on sexual and seven on asexual propagation, are most excellently done and are right up to date ; it would be difficult to name any book that does them better. The importance of the testing, selection, and maintenance of healthy clones is stressed, and the vital necessity for continuing the re-examination of source plants for both health and trueness to type is underlined. The risk of sub-microscopical mutations of the chromosomal material is a warning that vegetative propagation may not guarantee complete freedom from variation and demands perpetual vigilance.

Extensive bibliographies come at the end of each chapter ; there are 84 references for the principles of seed propagation and 66 for the techniques ; 162 and 46 for cuttings, besides 15 books for supplementary reading. The authors' protégés are certainly expected to get down to work. But then, this is a large book about the very bases of horticulture.

The index is attractively definite in referring to one page, or at most two pages, unlike the intimidating chains of numerals too often seen. There are some 200 illustrations from photographs and drawings, all of good quality. The text is clear, the binding serviceable ; it is indeed an excellent work, particularly for students and those horticulturists wishing to understand the scientific basis of their art. Book prices, we are told, are becoming more realistic these days but the older student is still somewhat dismayed by them. The new student, we hope, will cushion the shock by an increased educational grant but in either case this is a very good "buy".

R.J.G.

NOTICE TO CONTRIBUTORS

1. All **manuscripts** should be in double-spaced typewriting, with a good margin, and should be addressed to the Editor, East Malling Research Station, near Maidstone, Kent, England. Papers must be written concisely. Historical reviews should be as short as possible and only such references to literature as bear directly on the subject should be included. Tables and illustrations, if any, must be only such as are absolutely essential for clear presentation.

2. Authors of papers containing extensive **numerical observations** should consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from Burlington House, London, W.1, price 6d. Arrangements have been made whereby original data too extensive for complete publication may be deposited at the British Museum (Natural History), London, S.W.7, or with the Royal Society of Edinburgh, 22 George Street, and thus be available for consultation by other workers. Full bibliographical reference to the publication in which the results are summarized must be supplied with the data.

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4. Where a paper is of a highly technical nature it should be preceded by a brief **synopsis,** in which its contents are simply and clearly stated for the benefit of non-technical readers.

5. **References to literature** may be by numbers (in brackets) in the text corresponding to a numbered list at the end of the paper or by the Harvard system (author's name and date of publication). By either method, the papers cited should be listed alphabetically according to authors' names, followed by the date of publication. The title of the paper should next be given in full, followed by contracted, but strictly intelligible, title of source of publication, the volume and page numbers. Authors are responsible for the accuracy of their lists of references and should check them carefully in both typescript and proof.

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